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MOVING A RUBBER HAND
– THE SENSE OF OWNERSHIP AND AGENCY IN BODILY SELF-RECOGNITION

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Moving a rubber hand –
The sense of ownership and agency in bodily self-recognition

THESIS FOR DOCTORAL DEGREE (Ph.D.)

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ABSTRACT

Most of us take for granted that our body is our body. One typically experiences one's body as something belonging just to oneself, as something that can only be "me". However, this has poses a fundamental problem in philosophy and psychology: how do we know that the body is our own? It has been suggested that two distinct experiences of our own body help us recognize it as such: the **sense of ownership**, that is the experience that a limb is part of one's body, and the **sense of agency**, that is the experience of being able to voluntarily control limb movement. In the present thesis we introduce a new version of the classical rubber hand illusion that is based on finger movements instead of stroking and systematically investigate how ownership and agency contributes to bodily self-recognition.

To induce "**the moving rubber hand illusion**" participants control the movements of the index finger of a right wooden model hand in full view by moving their own right index finger, which is hidden from view. The illusion is quantified subjectively with visual analogue rating scales and behaviourally as changes in manually indicated sensed hand position ("proprioceptive drift"). In 9 separate experiments involving a total of 352 healthy volunteers we first characterized the basic constrains of the illusion. Secondly, we examined the relationship of ownership and agency. And finally, investigate a possible relationship between the illusion and individual differences in delusion proneness (using Peter's Delusion Inventory).

Our results show that synchronized movements of the model's index finger and the participant's index can trigger a strong illusory feeling of ownership of the model hand and robust experience of agency. The moving rubber hand illusion is similarly strong as the classical version, and follows similar temporal, spatial and anatomical rules. Asynchronous seen and felt finger movements, a too great distance between the real and model hands (≥27 cm), or the model placed in an anatomically implausible position abolishes the ownership-illusion.

We also found that ownership and agency can be dissociated. Unlike ownership, agency can be experienced for the model hand when it is when placed in an anatomically implausible position. And ownership can be experienced irrespective of the hand moving actively or passively, so with or without agency. Furthermore only ownership, but not agency ratings correlate with the proprioceptive drift. Finally, we observed that delusion prone-individuals tend to give generally higher overall ratings on agency, when they experience the hand moved passively.

Collectively, these observations advance our understanding of how ownership and agency contribute to bodily self-recognition. Ownership and agency constitute different processes: Integration of spatio-temporally congruent signals from moving limbs determine the sense of ownership and a match of movement intentions and feedback determines the sense of agency. These results offer new ways to study bodily self-recognition both at the behavioural and neural level.

LIST OF PUBLICATIONS

I. Kalckert, A. and Ehrsson, H.H. (2012) Moving a rubber hand that feels like your own: a dissociation of ownership and agency. Frontiers in Human neuroscience Vol. 6 (40)

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ADDITIONAL PUBLICATION

I. Schmalzl, L., Kalckert, A., Ragnö, C., and Ehrsson, H.H. (2013). Neural correlates of the rubber hand illusion in amputees: A report of two cases. Neurocase

TABLE OF CONTENTS

Table of Contents

LIST OF ABBREVIATIONS

EEG	Electroencephalography
EMG	Electromyography
fMRI	Functional magnetic resonance imaging
GSR	Galvanic skin response
IPS	Intraparietal sulcus
PDI	Peter´s delusion inventory
PET	Positron Emission Tomography
PMv	Ventral premotor cortex
PPC	Posterior parietal cortex
RHI	Rubber hand illusion
SMA	Supplementary motor area

1 THE QUESTION OF SELF-RECOGNITION

1.1 INTRODUCTION

When we look down at our body, we always have the experience that we indeed look down at *our* body. When I am typing these words or turning the pages of this book when reading this thesis I experience that these are my hands in front of me. I usually do not question this experience. It is invariably present in every movement I make. I am this body and this body is me. However it is unclear how we actually come to this experience and a number of philosophers (like Descartes, Hume or Wittgenstein to name a few) throughout the centuries have puzzled over this question. So how do we recognize our self, how do we make the distinction between the external world and me?

In recent years, the field of cognitive neuroscience has also started to adopt these questions and researchers started to investigate the neural and cognitive basis of this ability to be aware of oneself (Blanke, 2012; Blanke & Metzinger, 2009; Churchland, 2002; Damasio, 1998; Feinberg & Keenan, 2005; Jeannerod, 2003; Newen & Vogeley, 2003; Vogeley & Fink, 2003). Over the past few decades a plethora of experiments have been performed to show just how unique this ability is. One well-known example comes from famous experiments in which a spot was placed on the forehead of toddlers and monkeys, and then they were placed in front of a mirror. At a certain age toddlers actually realize that instead of scrubbing the image in the mirror they should rather scrub on their own forehead to remove the dot. Non-human monkeys typically fail here and will continue to scrub the mirror image instead. These findings have been interpreted as a certain lack of self-recognition or self-awareness (Gallup, 1970).

Human infants seem to develop the ability to distinguish between self and external world very early on: another famous experiment was conducted by Bahrick and Watson (Bahrick & Watson, 1985) in which 5 old months toddlers were shown either live recordings of their own leg movements or pre-recorded and thus non-matching leg movements. Toddlers at that age already discriminate between the contingent and non-contingent images. Further research explored how toddlers detect contingency of movement and feedback and found that this ability is present from very early on (as early as 6 months of age) (Rochat, 1998; Rochat & Morgan, 1995). This led some researchers to propose a “contingency module” in the infant brain which allows them to develop self-awareness by seeking out contingent and non-contingent effects in the world (Gergely, 2004). In this view there should be a specific neuro-cognitive architecture, which is specialized in discriminating, processing, and gathering self-related information. Whether such a self-specific neuro-cognitive architecture exists in the human brain is currently debated (for further discussion see Apps & Tsakiris, 2013; Gillihan & Farah, 2005; Legrand & Ruby, 2009; Northoff et al., 2006; Northoff, Qin, & Feinberg, 2011).

1.2 MANY SELFS

The term ´self˝ can refer to many different things, depending on the field and purpose of the investigation. And unsurprisingly there are many different concepts that refer to what we call the self, including (but not limited to) a name, a memory, a character trait, and an action.

In his seminal work William James (1890) already distinguishes between a physical self, a mental self, and a spiritual self. Neisser later proposed five different kinds of selves: the ecological self, interpersonal self, extended self, private self, and the conceptual self (Neisser, 1988). Other concepts of self have been and used by several authors in recent years, like the sentient self (Craig, 2010) or Damasio´s proto and neural self (1999) to name a few. Strawson (in Legrand and Ruby, 2009) compiled up to 25 different definitions of the self, which are used in various fields and concepts. Gillihan and Farrah (2005) in their review of the literature make a distinction between the physical and the psychological self and came to the conclusion that there is no perfectly conclusive evidence for a specific self-function in the human brain.

The division between a physical and psychological self is often found in these attempts to conceptualize the self and seems to be useful not only to gain clarity on this matter, but also to define the scope of the present work. The psychological self refers to the personality traits of the person: the attitudes, habits, and worldviews. These are probably rooted in the memories and experiences accumulated over a life span that result in the person's individual biography and character (Burgess, Maguire, & O'Keefe, 2002; Fivush, 2011). The physical self refers to our knowledge of the shape and look of our body - which over time can change, grow or even gets smaller, but is always experienced as one´s own (Ehrsson, 2012).

Naturally we find here some subtle differences between definitions and some of these different concepts resemble each other. A thorough discussion of all these concepts is beyond the scope of this work and in the following I narrow down the focus on the physical self. So the focus is on the body we have or rather the body we are, which is always perceived as the own body and which is distinct from other objects and persons in the world.

1.3 THE BODILY SELF

Recent developments in the field of philosophy, psychology, and cognitive science highlighted the importance of one´s body for the conscious experience of the self (Berlucchi & Aglioti, 1997; Chiel & Beer, 1997; Chiel, Ting, Ekeberg, & Hartmann, 2009; Daprati, Sirigu, & Nico, 2009; S. Gallagher, 2000; 2005; Legrand & Ruby, 2009; Tsakiris, 2010; Wilson, 2002). This is an embodied view of cognition, in which the physical self — so our body — is not and cannot be separated from our cognitive functions. In this view, the body is regarded as the fundamental basis of our cognitive abilities. One important factor here is the interaction with the environment, which can be regarded as one major, if not the major purpose of our overall cognitive architecture. Many of our cognitive abilities might be rooted in this interaction with the world (Anderson, 2003; Glenberg, 1997; O'Regan & Noe, 2001; Merlau-Ponty, 1945). Critically, in this view, the body not only passively receives input from the world, but also actively seeks out for it. Perception is then an active undertaking and one´s body is in constant interaction with the environment (Gibson, 1986; Noe, 2006). Several researchers suggested that this interaction is actually needed to “make sense” out of our perceptions (Gallese & Metzinger, 2003; Held & Freedman, 1963; Held & Hein, 1963; O'Regan & Noe, 2001; Wexler & van Boxtel, 2005).

However, a new problem arises here. As the body moves, it will generate new perceptions. For example, when I bend my wrist, I will feel stretches of the skin or when I walk visual information will flow onto the retina. This generates a new problem for our perceptual apparatus and has been subject of discussion for centuries (see for example Helmholtz, 1867). At the core of this problem is that our perceptions are partially created by us: when I lift my arm to touch an object, I create new input from my muscles. I flex the muscles to bend the arm, and the skin around my joints stretches.

If I experience these sensations without my will, it could mean that someone else grabs my arm. Thus, we need to be able to distinguish which of those perceptions are actually coming from the external world and which are produced by me (Crapse & Sommer, 2008a,b; Holst & Mittelstaedt, 1950).

Therefore the problem of how we come to the experience of our own body in action and we perceive the constant feedback from our body (which are partially generated by ourselves), is important when we want to understand the process of self-recognition.

1.4 OWNERSHIP AND AGENCY IN BODILY SELF-RECOGNITION

So, how do we know that our physical body is *my body*? Gallagher (2000) proposed that the awareness of our self is mediated by two fundamental experiences: the experience of ownership and the experience of agency. The **sense of ownership** is the experience that "*my body is moving regardless of whether the movement is voluntary or involuntary*", whereas the **sense of agency** represents the experience "*that I am the one who is causing something to move*" (S. Gallagher, 2000; p. 15). At any given moment when we move, we experience both these sensations together. However that both these sensations represent different aspects of the movement can be shown by passive movements: when someone else grabs my arm and moves it around, then I can sense that it is my arm being moved around, but the movement I experience is not produced by me, and therefore, I do not sense that I am generating this movement. Thus, I am lacking a sense of agency over the movement, but still experience the arm as my own (i.e., I still have a sense of ownership over the arm).

However, in situations where we need to identify our body, we could use both these processes of ownership and agency to come to the conclusion that "this is my hand". If you imagine a situation where you look at a screen with a number of identical hands, then how would you identify the hand that is really *your hand*? One obvious first hint would be to take that hand that is closest to the position where I feel my hand to be. A match between the felt position of your hand and the visually observed hand can give rise to the feeling that this is *your hand*. This conclusion would be drawn on the congruency between different kinds of afferent information. Another way to solve this problem is something many people instinctively do when they, for example, discover themselves on a video screen. They do a quick movement and check if the one on the screen is doing the same. The hand that moves in the way you move is most likely your hand.

Both these ways of solving this problem can be translated into the framework of ownership and agency. To identify our own body we can rely on the match of the visual and somatosensory information from our body, which results in the experience of perceiving this hand to by my own hand (i.e., I have a sense of ownership). And we can rely on the feeling of being in control of the hand in question. When the hand I observe is under perfect control of my will, I come to the very same conclusion and identify the hand to be my own hand (i.e., I have a sense of agency).

Investigations aiming to understand how we perceive the body as your own face a particular challenge: they need to be able to manipulate the perception of the own body. However, as William James already formulated in the 19th century: "the same old body (is) always there" (James, 1890, p. 260). One cannot simply study situations of not having a body and having a body. Some first insights into these questions have been made by investigating the way amputees experience their own body after the loss of a limb. Many amputees experience phantom limbs: that is, they still perceive the lost limb and some even can control movements of the absent hand or foot (Gerstmann, 1958; James, 1887; Ramachandran & Hirstein, 1998; Ramachandran & Rogers-Ramachandran, 1996). However, an experimental tool is needed which allows a manipulation of these perceptions in a more controlled way. To this end researchers started to use various kinds of illusions that involve the body and thereby offer the possibility to explore the perceptual mechanisms underlying these experiences.

2 ON OWNERSHIP

2.1 INTRODUCTION

The rubber hand illusion represents a major breakthrough in the investigation of the perception of the own body. It allowed researchers to examine the experience of the own body in an experimental way with healthy participants, and to explore the perceptual rules underlying the sensation of perceiving the body as one's own. Botvinick and Cohen introduced this illusion in 1998: in this illusion, a fake, but realistic, rubber hand is placed in front of the participant and the participant´s real hand is occluded from sight (see Fig. 2-1). Then, both the rubber hand and participant's hand are touched simultaneously in the same place. When experiencing this stimulation for some time participants begin to feel the touch as if it was originating from the place where they see the rubber hand being touched (i.e., there is a referral of touch) and also feel as if the rubber hand becomes their own hand (i.e., there is a sense of ownership). Or in other words participants experienced the model hand to be their own (Botvinick, 2004; Botvinick & Cohen, 1998). This ground-breaking study showed that the sense of the body can be experimentally manipulated. One can induce this feeling of owning an artificial body part with a relatively simple procedure by providing visual and tactile stimulation to both hands. The simplest explanation is that the visual and tactile information must be bound together to overcome this initial conflict between the visually observed (model) hand and the felt position of participant´s (real) hand. This study sparkled a new interest in the perception of the own body and a plethora of studies investigated how and when the illusion arises (Ehrsson, 2012; Makin, Holmes, & Ehrsson, 2008; Tsakiris, 2010).

Figure 2-1: Illustration of the classical rubber hand illusion

2.2 AT THE LEVEL OF PSYCHOLOGICAL PROCESSES

The rubber hand illusion is an inherently subjective experience. Thus, the simplest way to experimentally quantify these experiences is to ask the participants specific questions regarding their experience, and let them rate the agreement or disagreement to such a statement on a visual-analogue scale or Likert scale. Studies commonly use two specific kinds of statements, which typically constitute the core of the experience in the rubber hand illusion: 1. The experience of ownership of the rubber hand, as if the rubber hand is the own hand or feels like a part of the own body (i.e. "*I felt as if the rubber hand is my own hand*"), and 2. The experience of referral of touch, as if the touch the participant feels originates from the place they see the rubber hand being touched (i.e. "*I felt as if the touch I felt was caused by the brush touching the rubber hand*"). Both these aspects of the illusory experience are commonly evaluated to measure the presence or absence of the illusion. The exact relationship of these two experiences (i.e., ownership and referral of touch) is not clear yet. It is also common practice also to include control statements, so statements that do not reflect the sense of ownership, but refer to a rather unrelated sensation (e.g., "*My hand was turning rubbery*"). This is a good way to control for task compliance or unspecific responses of the participants.

However, more objective measurements have been introduced to register the illusion. Botvinick and Cohen (1998) already measured whether participants felt their real hand to be closer to the rubber hand during the illusion. As the participant cannot see their own hand they have to rely solely on the "felt" position when making judgments about the location of the hand. Many studies use this approach to measure the felt "proprioceptive drift" of the stimulated hand during the illusion (Kammers, Longo, Tsakiris, Dijkerman, & Haggard, 2009; Preston, 2013; Riemer, Kleinböhl, Hölzl, & Trojan, 2013; Tsakiris & Haggard, 2005b; Tsakiris, Hesse, Boy, Haggard, & Fink, 2007a), which has often been found to be correlated with the subjective strength of the illusion (Botvinick & Cohen, 1998; Kalckert & Ehrsson, 2012; Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008). More recently, other studies have found that the drift might not be a specific measure of the illusion, and can be present in situations in which no illusion is present (Folegatti, Farnè, Salemme, & de Vignemont, 2012; Holle, McLatchie, Maurer, & Ward, 2011; Holmes, Snijders, & Spence, 2006; Rohde, Di Luca, & Ernst, 2011). An inherent problem in comparing the drift measure across studies is the exact procedure. Some studies use perceptual judgments, for which participants have to judge the felt position of the unseen hand in relation to a visually presented ruler (Tsakiris, Prabhu, & Haggard, 2006). In other studies participants are instructed to point or reach to the felt position with the hand that is not stimulated (Kalckert & Ehrsson, 2012). A recent study (Riemer et al., 2013) showed that a perceptual judgment versus manual procedure might result in a different performance, making it difficult to compare results across studies.

Another way to objectively measure the illusion is the skin-conductance response to a physical threat to the rubber hand. Here, the galvanic skin response (GSR) is measured with an electrode recording the conductivity of the skin that changes with sweating. When faced with an emotionally salient stimulus the physiological response leads to an increase in sweating and an increase in conductivity (Dawson et al, 2000). Armel and Ramachandran (2003) introduced this method by bending the rubber hand's finger into anatomically impossible positions and found that participants react stronger when they feel ownership over the hand, as compared to control conditions (Armel & Ramachandran, 2003). Other studies have threatened the rubber hand with a knife or syringe (Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007; Guterstam, Petkova, & Ehrsson, 2011). Ehrsson and colleagues (2007) found that emotional circuits involving the anterior insula and anterior cingulate cortex respond during the illusion when the rubber hand is threatened. This provides further evidence for a genuine emotional response to the rubber hand threat, when it is perceived to be part of the own body (Ehrsson et al., 2007).

By using these different procedures to quantify the illusion a number of studies investigated the perceptual rules underlying the illusion (Ehrsson, 2012; Makin et al., 2008; Tsakiris, 2010). These studies have repeatedly found that the illusion is not induced when the stimulation is asynchronous, so when the brush stroke on the hand and the visually observed brush stroke to the rubber hand do not match in time (Botvinick & Cohen, 1998; Ehrsson, Spence, & Passingham, 2004; Shimada, Fukuda, & Hiraki, 2009a; Tsakiris & Haggard, 2005b). Therefore the timing of the two sensory inputs (i.e., the touch to the real hand and the visually observed touch to the rubber hand) must coincide. Synchronously applied visuotactile stimulation is one crucial factor.

Also spatial factors like the distance between the participant's hand and the rubber hand — which is in most cases approximately 10-15 cm — are crucial. It has been shown that when the distance between the two hands increases, the illusion gets weaker or even disappears entirely (Lloyd, 2007; Preston, 2013). Lloyd (2007) showed that by moving the rubber hand more than 27.5 cm away from the participant´s real hand, the illusion is substantially reduced (as measured by a referral of touch statement). Other studies did not find an effect of distance (Armel & Ramachandran, 2003; Zopf, Savage, & Williams, 2009). Furthermore Preston (2013) showed that not only the distance of the two hands is critical, but also the relative distance of the rubber hand to the body (i.e., to the trunk) affects the illusion. Therefore the exact role of distance is not entirely clear and the difference in results obtained so far might be influenced by other factors like the specific arrangement of the two hands (e.g., lateral versus distal) or distance to the body.

Another factor is also the posture of the hand: Lloyd (2007) not only varied the distance (medially to the participant`s right hand), but also increasingly rotated the hand (as if the right hand would reach over to the left side). For example, when the posture of the real hand is rotated to a 90° or 180° with respect to the rubber hand the illusion is not evoked (Ehrsson et al., 2004; Ide, 2013; Tsakiris & Haggard, 2005b). This could also affect the illusion, as several studies have shown that the rubber hand has to be in alignment with the participant´s arm, so in an anatomically plausible posture with respect to the participant´s arm.

Based on those observations one can formulate some basic perceptual rules for the rubber hand illusion: (1) that the stimulation needs to occur in temporal synchronicity (i.e., *temporal rule*), and (2) that the stimulation must originate from the same region in space (i.e., *spatial rule)*. These rules remind us of principles found in multisensory integration (Holmes & Spence, 2005; Stein & Stanford, 2008). Moreover the rubber hand needs to be positioned in a congruent posture (*anatomical plausibility*). When any of those principles are violated, the illusion is substantially reduced or eliminated.

Other studies examined further aspects of the illusion. For example, the stimulation needs to occur in hand-centred reference frames. Thus the stroking direction of the two brush strokes should be in agreement with respect to the hands, and not in head-centred reference frames (Costantini & Haggard, 2007). Also, not any object can be used: a block of wood without any resemblance to a human hand or a left hand instead of a right hand will not elicit the illusion (Guterstam et al., 2011; Tsakiris et al., 2007a; Tsakiris, Carpenter, James, & Fotopoulou, 2010a). This is probably mediated by a top-down knowledge about of which objects can be potentially part of the body (Tsakiris et al., 2010a; Tsakiris & Haggard, 2005b). It shows that this process cannot be purely bottom-up driven by sensory input, and that certain a priori criteria need to be fulfilled to perceive the illusion of ownership. Surprisingly, the illusion evolves rather quickly: Lloyd (2007) measured the time it takes for participants to report a referral of touch sensation and found it takes, on average, only about 5 sec. Furthermore, Ehrsson and colleagues (2004) found that that the time it took for participants to indicate when they experienced ownership of the rubber hand was only about 11 seconds.

The principles found in the rubber hand illusion have been also used in experiments to create new versions of illusions: the somatic rubber hand illusion, where participants touch a rubber hand while their own hand is touched (Ehrsson, Holmes, & Passingham, 2005), and the invisible hand illusion, where the empty space is touched while the participant is touched on the hand (Guterstam, Gentile, & Ehrsson, 2013). Interestingly the illusion can even lead to the illusory experience of three arms (Ehrsson, 2009; Folegatti et al., 2012; Guterstam et al., 2011). The illusion is not restricted to the hand and can also be extended to the whole body making participants perceive a mannequin body to be their own body (Petkova & Ehrsson, 2008; Petkova et al., 2011a). These principles can be also applied to create out-of-body experiences, causing participants to feel relocated to a place outside their body (Ehrsson, 2007; Lenggenhager, Tadi, Metzinger, & Blanke, 2007). Another paradigm uses the face watched in a mirror-like setup in which a different face is viewed and touched in synchrony with the own face (Tsakiris, 2008). Virtual-reality techniques have also been used to create bodily illusions (Perez-Marcos, Slater, & Sanchez-Vives, 2009; Slater, Perez-Marcos, Ehrsson, & Sanchez-Vives, 2008; Slater, Spanlang, Sanchez-Vives, & Blanke, 2010).

2.3 AT THE LEVEL OF BRAIN PROCESSES

A few neuroimaging studies have investigated the neural mechanisms of the rubber hand illusion in the human brain. Ehrsson and colleagues (2004) used fMRI to examine the neural correlates of the illusion: here, the ventral premotor cortex (PMv) and the intraparietal cortex (IPS) were specifically activated during the illusion, as compared to control conditions, in which the hand was stimulated asynchronously or the rubber hand was rotated. These regions are known to be involved in the processing of multisensory stimuli, in particular visual and tactile signals from the hand (Gentile, Petkova, & Ehrsson, 2011; Lloyd, Shore, Spence, & Calvert, 2003). Intriguingly the activity of the PMv was correlated to the subjective strength of the illusion. Activations of the cerebellum and dorsal premotor cortex were also observed in the period before the illusion onset (i.e., in the phase where the potential recalibration of position sense is taking place).

Another functional imaging study, which has investigated the neuronal mechanisms of the rubber hand illusion, was conducted by Tsakiris and colleagues (2007) using PET. They found activations of the posterior insula that showed a positive correlation with the proprioceptive drift measure across the conditions. The insular cortex has been shown to be prominently involved in aspects of interoceptive awareness like nociception or thermosensation (i.e., in functions related to the physiological and emotional regulation of the body) (Björnsdotter, Loken, Olausson, Vallbo, & Wessberg, 2009; Craig, 2003; Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004; Löken, Wessberg, Morrison, McGlone, & Olausson, 2009; Penfield & Faulk, 1955). The role of the insula in body awareness has also been implicated in studies with neurological patients, who suffer from disorders that affect their perception of the body (Baier & Karnath, 2008; Karnath & Baier, 2010).

A number of neuroimaging studies have shown that both the ventral premotor cortex and posterior parietal cortex are involved in multisensory integration, and in particular of visual and tactile input (Bremmer et al., 2001; Gentile et al., 2011; Lloyd et al., 2003; Makin, Holmes, & Zohary, 2007; Schlack, Sterbing-D'Angelo, Hartung, Hoffmann, & Bremmer, 2005). More recently, studies have shown that both these structures are involved in visuotactile integration and specifically for the hand, and in the ownership illusion (Brozzoli, Gentile, & Ehrsson, 2012; Brozzoli, Gentile, Petkova, & Ehrsson, 2011; Gentile, Guterstam, Brozzoli, & Ehrsson, 2013). These studies further examined the role of the PMv and PPC and found again that the activity of the PMv was correlated to the subjective strength of the illusion, and the PPC activity was correlated to the proprioceptive drift. Therefore both these structures might perform different aspects within the neural processes underlying the illusion.

Other variations of the rubber hand illusion like the somatic rubber hand illusion (Ehrsson et al., 2005) or invisible hand illusion (Guterstam et al., 2013) similarly result in activations of a premotor-posterior parietal network. Further support for the role of this network in the generation of the ownership sensation comes also from the full-body illusion (Petkova & Ehrsson, 2008). During this illusion the ventral premotor and posterior parietal cortex, as well as other structures like the putamen are activated (Petkova et al., 2011a). This network of the premotor and parietal cortex is coherent with findings from neurophysiological studies on multisensory integration (Graziano & Botvinick, 2002).

2.4 AT THE LEVEL OF NEUROPHYSIOLOGICAL PROCESSES

A key feature of the illusion is the integration of vision and touch. The merging of the senses (i.e., multisensory integration) has been abundantly studied with neurophysiological techniques, and in a variety of species, including the cat and non-human primates (Meredith, 2002; Stein & Stanford, 2008). These studies explored the rules governing the responses of neurons to multisensory stimuli in various cortical structures like the posterior parietal and premotor cortex, and other subcortical structures like the putamen or superior colliculus (Duhamel, Colby, & Goldberg, 1998; Fogassi et al., 1996; Graziano & Gross, 1993; Graziano, Cooke, & Taylor, 2000; Hyvärinen, 1981; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981a; 1981b). These studies found that there are neurons in these regions that integrate visual and tactile input. So the neuron responds to a tactile stimulus to the hand, and a visual stimulus close to the hand. Such a bimodal neuron responds then in an additive or super-additive fashion. This indicates that these neurons are particularly tuned to the co-occurrence of both stimuli, insofar as they originate in the same region of space and occur sufficiently close in time (Holmes & Spence, 2005; Stein & Stanford, 2008). Importantly, the receptive field of such neurons moves with the body part. When the location of the hand changes, also the visual receptive field relocates with the hand and is then responsive to a stimulus close to the hand´s new position. Thus, these bimodal cells encode space near the body in body-part centred coordinates (Graziano, 1999; Graziano, Hu, & Gross, 1997).

In sum, the principles found in these neurophysiological studies fit rather well with observations from the rubber hand illusion, as the illusion seems to follow perceptual rules reminiscent of multisensory integration and draws on similar neural mechanisms (Brozzoli, Ehrsson, & Farnè, 2013; Ehrsson, 2012; Maravita, Spence, & Driver, 2003). Therefore, it seems reasonable to assume that neurons with these features are involved not only in the rubber hand illusion, but also in the perception of our own body.

3 ON AGENCY

3.1 INTRODUCTION

The sense of agency is difficult to define as it encompasses a variety of psychological aspects and mechanisms. For example, Balconi (2010) lists “awareness of a goal, of an intention to act, and initiation of action, as well as awareness of movements, sense of activity, sense of mental efforts, sense of control, and the concept of authorship” (p. 3) as putative components of the sense of agency. All these different aspects contribute to our experience of agency, when we perform an action. Unsurprisingly the literature on the sense of agency includes a variety of observations and theoretical frameworks and often relates to other questions like the nature of free will (Haggard, 2008; Hallett, 2007; Synofzik, Vosgerau, & Newen, 2008b; Wegner, 2003)

In a broader view, the sense of agency can be used as a means to answer the question “was that event generated by myself or by someone else in the world”? The environment around us is usually not static, but constantly changes and provides endless sets of new sensory information. Some of these changes are changes caused by myself, as I move and act in the environment. Therefore the ability to classify whether these changes are actually caused or someone else is important. Helmholtz elaborated on this problem already in 19th century by discussing the observation that when the eyeball is moved passively, the image on the retina actually jumps. However we do not perceive this when we normally move the eyes (Helmholtz, 1867). Therefore the information from the eye must be somehow adjusted to the upcoming eye movement, so we know that these changes on the retina are changes that are a direct result of my movement and not from the outside world. This in principal must not only apply to the eye, but to our whole body.

Later, in the 1950s von Holst & Mittelstädt (1950) and Roger Sperry (1950) re-approached this problem from a more biological perspective. They suggested that a copy of the motor commands (i.e., efference copy) entailing the expected sensory changes could be used to classify perceptions into input that is the result of the own action (i.e., re-afference) or an input that originated from the external world (i.e., ex-afference) (Bell, 1981; Crapse & Sommer, 2008a,b; Holst & Mittelstädt, 1950;

Sommer & Wurtz, 2002; Sperry, 1950). This provides a key mechanism that can discriminate between sensations generated by me and by someone or something else.

3.2 AT THE LEVEL OF PSYCHOLOGICAL PROCESSES

A key factor in the sense of agency is the congruency between an action and its feedback, so the anticipated outcome compared to the actual outcome. Therefore, many studies investigating the sense of agency typically manipulate the feedback (i.e., visual or auditory feedback) of an action (Balslev, Cole, & Miall, 2007; Daprati et al., 1997; de Vignemont & Fourneret, 2004; Farrer, Bouchereau, Jeannerod, & Franck, 2008a; Franck et al., 2001; Haggard & Chambon, 2012; T. I. Nielsen, 1963; Preston & Newport, 2010; Sato & Yasuda, 2005; Tsakiris, Haggard, Franck, Mainy, & Sirigu, 2005). For example, when the delay between a button press and a subsequent tone increases, the participant´s sense of having caused this tone gradually decreases. A reduction in the sense of agency is also observed when the tone has a different frequency than the tone anticipated by the participant (Sato & Yasuda, 2005). In addition to temporal deviations, also spatial deviations have also been found to alter the sense of agency. For example, when the visual feedback of a cursor or joystick movement is spatially distorted, then similar a reduction of agency is observed (Farrer, Bouchereau, Jeannerod, & Franck, 2008a; Franck et al., 2001). Studies investigating the spatiotemporal rules of the sense of agency have found that the threshold at which we still experience an action as our action is a temporal delay of ~150 ms and a spatial deviation of 15-20°. Beyond these discrepancies participants begin to judge the feedback to be inaccurate with regard to their expectations (Jeannerod, 2003; Shimada et al., 2009a).

One very influential account of these observations is based on the framework of motor control (Bays & Wolpert, 2006; Franklin & Wolpert, 2011; Wolpert, 1997; Wolpert & Ghahramani, 2000). To achieve accurate control the motor system does not only use sensory feedback, but also uses predictions (i.e., forward models), which are compared to the actual feedback. A discrepant feedback would signal to the motor system the necessity to monitor and correct the movement accordingly. Indeed, the role of these predictive processes in motor control has been shown in a variety of tasks (Bays, Wolpert, & Flanagan, 2005; Desmurget & Grafton, 2000; Flanagan, Vetter, Johansson, & Wolpert, 2003; Johansson & Flanagan, 2009; Shergill, Bays, Frith, &

Wolpert, 2003). These efference copy mechanisms might also be the basis for the psychological experience of agency (Blakemore & Frith, 2003; Blakemore, Wolpert, & Frith, 2002; Frith, Blakemore, & Wolpert, 2000b; Haggard, 2005). However, it has been found that this framework cannot fully explain all observations of the sense of agency. Several studies found that in some circumstances participants can perceive agency even in cases of rather large spatiotemporal discrepancies (Fourneret & Jeannerod, 1998; Nielsen, 1963; Preston & Newport, 2010).

This led some researchers to suggest that our experience of actions does not just depend on the exact sensorimotor contingencies, but also on a more general congruency between intention and actions (Wegner & Wheatley, 1999; Wegner, 2002). And indeed this account can explain some observations in which participants experience a sense of agency when the action is actually not causally linked to that stimulus. For example, Wegner and colleagues (2004) presented participants auditory primes via headphones while they saw the outstretched arms of the experimenter (standing behind them) sticking out in the front of the participant. The experimenter then executed actions (like wave your hand) while the participants heard the same word. When the word and the observed action are congruent, then participants actually feel to have caused those arms to move the way they moved (Wegner, Sparrow, & Winerman, 2004). In these cases the experience of agency cannot be derived from sensorimotor contingencies or any feeling of doing and must be therefore inferred from other non-sensorimotor cues.

A fundamental problem in the sense of agency literature is the heterogeneity of the experimental approaches (David, 2012; David, Newen, & Vogeley, 2008; S. Gallagher, 2012; Haggard & Chambon, 2012; Jeannerod, 2003). Gallagher (2007) pointed that authors are often conceptually unclear about what exactly they are referring to when they manipulate agency. Depending on the actual task demands (i.e., judgement of feedback from hand movements versus cursor movements) agency might be perceived differently and might be judged on the basis of different kinds of information (Farrer, Valentin, & Hupé, 2013; Preston & Newport, 2010; Sato, 2009; Synofzik, Vosgerau, & Newen, 2008a; Yomogida et al., 2010). The question whether agency is based on sensorimotor contingencies or mere intention is one reason for the heterogeneity in the literature (S. Gallagher, 2012; Synofzik, Vosgerau, & Newen, 2008a; Tsakiris & Haggard, 2005a). Tsakiris and Haggard (2005a) pointed out that in essentially all agency paradigms the participant needs to move. Thus sensorimotor contingencies are always present, and it is difficult to isolate the contribution of afferent and efferent information in the experience of an action.

One way to reconcile these different observations is to distinguish between different levels of agency. Several distinctions have been proposed, such as pre-reflective versus reflective agency (S. Gallagher, 2012), implicit versus explicit agency (Moore, Middleton, Haggard, & Fletcher, 2012), or feelings versus judgements of agency (Synofzik, Vosgerau, & Newen, 2008a). At the core of these distinctions is the idea that agency cannot be only derived from sensorimotor contingencies, but also from environmental or contextual cues. Therefore one must consider a multifactorial process in the sense of agency, so that agency can arise by sensorimotor contingencies weighted against contextual information. When contextual information or the intention to achieve a certain goal is valued higher, then sensorimotor discrepancies can be disregarded and participants still perceive agency by integrating these other cues (Farrer et al., 2013; J. Moore, Wegner, & Haggard, 2009; Sato, 2009; Synofzik, Vosgerau, & Newen, 2008a).

An inherent difficulty in investigating the sense of agency is to find an objective way to measure it. An interesting phenomenon, which has been suggested to be an implicit measure of the agency experience, is the so-called temporal binding effect (Haggard, Clark, & Kalogeras, 2002; Moore & Obhi, 2012). When participants judge the onset of their action and the subsequent result (e.g., a beep tone), then these judgements are temporally biased such that the action seems to occur later than it actually did and the beep tone to occur earlier than it actually did. In this way, the action and the tone appear to be closer together in time, as if the participants experience those two events to be temporally bound (Moore & Obhi, 2012). This temporal binding is specific to voluntary actions, and does not occur during passive movements. This is consistent with the idea that this phenomenon is related to the sense of agency.

3.3 AT THE LEVEL OF BRAIN PROCESSES

Given the variety of concepts and components I have described above, it is not surprising that there a number of different brain areas that have been found to be involved in the sense of agency (David et al., 2008). Among these, I will highlight a few structures that are repeatedly observed in agency paradigms. These seem to be related to key aspects of the sense of agency like movement intention and processing of sensory feedback.

One highly relevant structure is the supplementary motor area (SMA) (Picard & Strick, 2001). The SMA is critically involved in the initiation of an action, or the intentional aspect of the action (Eccles, 1982; G. Goldberg, 1985; Jahanshahi, Jenkins, Brown, & Marsden, 1995; Jenkins, Jahanshahi, Jueptner, Passingham, & Brooks, 2000; Lau, Rogers, Haggard, & Passingham, 2004; Roland, Skinhøj, Lassen, & Larsen, 1980). Activation of the SMA has also been observed when comparing active and passive movements (Mima et al., 1999; Weiller et al., 1996), which is an elegant way to differentiate between afferent and efferent components (Cullen, 2004). These studies show, among others, activation of the SMA in active movements. Studies on voluntary movement execution using other techniques like electroencephalography (EEG) have also shown heightened activity localized to frontal midline structures around the SMA (Haggard, 2008; Hallett, 2007; Libet, Gleason, Wright, & Pearl, 1983).

Another important cortical structure is the posterior parietal cortex, which is known to be involved in a variety of tasks related to visuomotor and visuospatial transformations (Culham & Valyear, 2006; Fogassi et al., 2005). Studies making use of a mismatch detection task have repeatedly shown that increasing sensorimotor discrepancy (i.e. the visual feedback is delayed with respect to the actual movement) is associated with increasing activity in the inferior parietal cortex, and in particular angular gyrus (Balslev, Nielsen, Paulson, & Law, 2005; Farrer et al., 2003; Farrer, Frey, Van Horn, Tunik, Turk, et al., 2008b; Nahab et al., 2011). Thus, this structure seems to be important in the detection of such sensory mismatches, and might also mediate between conflicting sensory input (Hagura et al., 2007).

Similar to the posterior parietal cortex, the cerebellum has been implied in the processing of sensory feedback (Blakemore & Sirigu, 2003; Manto et al., 2011). In a series of experiments Blakemore and colleagues tested how participants perceived self-produced stimuli, which are perceived to be weaker than externally produced stimuli (Blakemore, Wolpert, & Frith, 2000b). This is nicely exemplified by the famous question, “why I cannot tickle myself” (Weiskrantz & Elliott, 1971). These experiments suggested that the cerebellum is involved in the sensory predictive process resulting in the cancellation of self-produced stimuli (Blakemore, Frith, & Wolpert, 2001; Blakemore, Wolpert, & Frith, 1998). Together, these and other studies show that the cerebellum is involved in the predictive component in motor control (Ebner & Pasalar, 2008).

Most agency studies make use of a mismatch detection paradigm and measure the neural responses as the discrepancy between movement and feedback increases. However, this leads us to a conceptual problem: these brain areas signal the increasing discrepancy (Nahab et al., 2011), and are therefore active when in fact the participant does not feel agency. An exception to this is a study by Farrer and Frith (2003), in which they investigated not only the neural responses for increasing discrepancy (leading to activation of the inferior parietal cortex), but also for congruent feedback, so (i.e., for those movements where participants so feel agency). They found that when participants experience temporally congruent feedback, the activity in the right posterior insula was increased.

3.4 AT THE LEVEL OF NEUROPHYSIOLOGICAL PROCESSES

Electrophysiological studies in the monkey brain have investigated various aspects of sensorimotor control that are relevant for the sense of agency. These studies confirm the role of the SMA in movement initiation. The function of the SMA became clearer, when studies examined the specific role of neurons in different locations of the medial motor areas (Picard & Strick, 1996). The medial motor region consists of a number different motor areas, most notably of the SMA-proper and pre-SMA (Geyer, Matelli, Luppino, & Zilles, 2000; Luppino & Rizzolatti, 2000). Whereas the SMA-proper shows corticospinal projections and is densely connected to other premotor areas, the pre-SMA is more connected to prefrontal areas (Mitz & Wise, 1987; Picard & Strick, 1996; Tanji & Kurata, 1979). This difference in connectivity also illustrates the different functional roles in motor tasks. The SMA-proper is more related to the execution of movement and the pre-SMA is more related to the initial planning of movements (Hoshi & Tanji, 2004).

Neurons in the posterior parietal cortex are involved in a variety of motor or visuomotor related tasks (Andersen & Cui, 2009; Cooke, Taylor, Moore, & Graziano, 2003; Hyvärinen, 1982). Andersen and colleagues studied neurons in the parietal cortex and their role for saccades and eye movement control. They found neurons in the posterior parietal cortex encode the upcoming saccades, thus which movement is intended to be executed next. This has been interpreted in a way that neurons in this area form intentional maps (Andersen & Buneo, 2002; Snyder, Batista, & Andersen, 1997).

A role of the PPC for movement intention has also been suggested by a study with brain surgery patients. Desmurget and colleagues (2009) electrically stimulated the ventral premotor and inferior parietal cortex, while at the same time measuring the electromygraphic (EMG) activity of a number of muscle groups. Interestingly, while stimulation of the premotor cortex led to contractions of muscles, patients did not report the sensation of having caused these movements. In contrast, stimulation of the inferior parietal cortex did not result in muscle activity, but patients reported having the urge to move (or claimed to have moved) (Desmurget et al., 2009). Already Wilder Penfield in his pioneering studies reported that electrical stimulation of the cortical surface can induce the urge to move or sensations of having moved, but he found similar responses rather after stimulation of precentral areas (Penfield, 1954; Penfield & Boldrey, 1937).

Although, I have mostly emphasised here cortical structures for movement initiation also sub-cortical structures (e.g., basal ganglia) have also been found to be important in the voluntary generation of movements (Grillner, Hellgren, Ménard, Saitoh, & Wikström, 2005; Penfield, 1954). The basal ganglia are connected to the SMA, but also to the parietal cortex and the cerebellum, and therefore play an important role in motor control (Akkal, Dum, & Strick, 2007; Clower, Dum, & Strick, 2005; Graybiel, 2005; Hoshi, Tremblay, Féger, Carras, & Strick, 2005). All those different structures typically implied in the sense of agency (i.e., SMA, PPC, Cerebellum) are functionally and anatomically linked, thereby building a densely connected network involved in motor control (Dum & Strick, 2005; Grefkes & Fink, 2005; Luppino & Rizzolatti, 2000; Ramnani, 2006; Rizzolatti & Luppino, 2001).

4 SELF-RECOGNITION, OWNERSHIP AND AGENCY

4.1 SELF-RECOGNITION OR OWNERSHIP OR AGENCY

Given the variety in concepts of self or self-recognition, it is not surprising that the literature appears rather heterogeneous. Studies often use very different concepts and apply different tasks to explore the mechanisms involved in self-recognition.

4.1.1 The problem of self-recognition

Many studies investigating self-recognition use pictures or other stimuli related to the person, and the participant has to judge whether this stimuli can be attributed to him or herself (e.g., a picture of the participant). Several authors criticised that the recognition on screens, pictures, and mirrors (i.e., in the aforementioned study by Gallup, 1970) is falsely taken as evidence for self-awareness or self-recognition and that extrapolation from one medium to another (e.g., mirror to video) is problematic. Familiarity with the medium might affect the performance in such a task (Heyes, 1995; Suddendorf & Butler, 2013). Therefore, with studies using these kinds of media it is not certain whether the performance is an artefact of the technique used.

Furthermore, Legrand and Ruby (2009) argued that studies using self-related stimuli never actually tap into self-specific mechanisms. These might refer to the identity or personality to the person, but "*none of these contents can be considered intrinsically self-specific: They do not meet the criterion of exclusivity*" (p. 272). These stimuli are not exclusive as many people can have black hair or be shy, but that does not mean that having black hair or being shy is unique to this individual. Interestingly, the authors suggest that the feeling or experience of the own body could be regarded as one of a few instances that are exclusively and specifically related to the self. No one can experience *my* body the way I experience it.

A critical factor here might be the perspective. Most often stimuli are viewed from a third-person perspective. However we perceive our self always from the first-person perspective, so from "within". This perspective constitutes the basis of our self-experience (Legrand & Ruby, 2009; Vogeley & Fink, 2003). In line with this it has been shown that this first-person perspective is crucial to induce illusions like the full-body illusion, in which participants perceive a mannequin's body as their own body. When the perspective changes, so participants view the body from a third-person perspective, the illusion is significantly reduced (Petkova et al., 2011a; Petkova, Khoshnevis, & Ehrsson, 2011b).

Recent technological developments in video technology, for example head – mounted displays (Petkova et al., 2011a; Petkova & Ehrsson, 2008), high-performance video systems (Newport, Pearce, & Preston, 2010; Preston & Newport, 2010), and virtual-reality techniques (Perez-Marcos et al., 2009; Sanchez-Vives, Spanlang, Frisoli, Bergamasco, & Slater, 2010; Slater, Perez-Marcos, Ehrsson, & Sanchez-Vives, 2009) can overcome some of these aspects by generating a more natural first person-experience and induce a realistic and "immersive" experience (Slater, 2009). Still one has to take into account that neuro-cognitive mechanisms might respond differently to virtual or real stimuli (Perani et al., 2001; Snow et al., 2011). This applies also to paradigms like the rubber hand illusion. It has been found that the illusion is weaker when not a real, but projected or video-based hand image is used instead (Ijsselsteijn, de Kort, & Haans, 2005)

In sum, one should carefully distinguish between (visual) self-recognition paradigms using pictures, mirrors or video images and paradigms like the rubber hand illusion that involves a somatic experience of the rubber hand being part of the own body. Self-recognition here is a result of a different set of mechanisms and factors related to the feeling of ownership, which are not necessarily implied in other self-recognition paradigms.

4.1.2 Agency with or without ownership

Many studies use a mismatch detection paradigm, in which the image of the hand is displayed on a screen and the spatiotemporal characteristics of the hand movement are manipulated (Daprati et al., 1997; Nahab et al., 2011; Tsakiris et al., 2005). These implicitly assume that this will make the task more self-specific, as if it is the participant´s own hand. However, in some of these cases it can be questioned whether this really involves the bodily experience of ownership, like in the rubber hand illusion. Sometimes the assumption of measuring agency specific to the own hand is more implicit (e.g., Nahab and colleagues (2011) aiming to "*characterize the neural* *mechanisms underlying self-agency*") or explicitly assumed (e.g., Shimada and colleagues (2009) who argue that they "*can consider that the subject would feel the sense of ownership*"). Often this question is actually not raised at all. Sometimes it is even likely that the participants might experience body ownership due to the specific arrangement of the experiment resulting in a match of the visually observed hand and felt position of the participant´s hand, e.g., in Farrer and Frith (2003). Many of these studies do not clearly operationalize ownership and agency in a way that allows measuring their individual contribution to the self-recognition task.

Even when these studies consider ownership and agency, they might tap into a new problem. As pointed out by Tsakiris and colleagues (2007a) in any observation in these paradigms it might not be possible to clearly identify which aspect – ownership or agency – actually contributes to the self-recognition judgment. A mismatch between the own action and the observed hand will cause two different types of error signals: an error signal indicating that there is a violation of the prediction (i.e., the observed hand is not moving as it was predicted = *motor prediction error = agency error*), but also a mismatch between the felt position of the hand and the visually displayed hand (i.e., the observed hand is not at the position I sense it = *intersensory error = ownership error*). Both these errors will indicate that the observed hand is not the *own* hand (Tsakiris, Longo, & Haggard, 2010b; Tsakiris, Schütz-Bosbach, & Gallagher, 2007b).

Following this line of thought we have to conclude that any self-recognition judgment in a broader sense could be based on either ownership or agency related cues. Vice versa we have also to conclude that when a participant shows an abnormal performance in a self-recognition task (i.e., falsely identifying the observed hand as the own despite gross mismatches), we cannot be sure where the actual disturbance comes from: from faulty agency or from faulty ownership cues. Both can be interpreted as errors in self-recognition.

4.2 SELF-RECOGNITION IN NEUROLOGICAL AND PSYCHIATRICAL POPULATIONS

The aforementioned problem applies also to observations in clinical populations. Altered perceptions of the body have been discussed from the very beginning of modern psychology and neurology (Bonnier, 1905 (2009); Gerstmann, 1927; Pick, 1922; Smythies, 1953; Zingerle, 1913). These disturbances can affect various aspects of the perception of the own body resulting in a variety of sometimes bizarre symptoms reported by patients (Corradi-Dell'Acqua & Rumiati, 2007; de Vignemont, 2009; Vallar & Ronchi, 2009). Some of these syndromes are of particular interest as they might reflect a disorder of the sense of ownership and / or agency.

A prominent example for a disorder affecting self-recognition is schizophrenia, for which altered experience of the self and self-recognition are hallmarks of the disorder (Hur, Kwon, Lee, & Park, 2013; Jeannerod, 2009; Nelson et al., 2009; Parnas, 2005; Waters & Badcock, 2010). For a long time it is believed that many of these symptoms can be summarized under agency failures rooted in dysfunctional comparator mechanisms (Feinberg, 1978; Frith, 1996; Frith, Blakemore, & Wolpert, 2000a), despite the fact that schizophrenic patients often exhibiting a variety of abnormal perceptions of their own body that are unrelated to the sense of agency (Cleveland, Fisher, Reitman, & Rothaus, 1962; Fisher, 1964; Gerstmann, 1958; Priebe & Röhricht, 2001; Röhricht & Priebe, 1997). Nevertheless, in line with the idea of an abnormal sense of agency and faulty efference copy mechanisms studies using mismatch detection paradigms have found that schizophrenic patients are not as sensitive for temporal delays or spatial deviations as healthy participants (Daprati et al., 1997; Farrer et al., 2004; Franck et al., 2001). They also show abnormal sensory predictions (Blakemore, Smith, Steel, Johnstone, & Frith, 2000a; Shergill, Samson, Bays, Frith, & Wolpert, 2005).

Given the intimate linkage between agency and ownership in voluntary movements the questions arises as to whether schizophrenia must be understood solely as a disorder of agency and whether the pathology affects self-processing in broader way (Parnas, 2005; Raballo, Saebye, & Parnas, 2011). As pointed out by Waters and Badcock (2011) a self-attribution deficit (as observed in these mismatch detection paradigms, see e.g., Daprati et al., 1997) can be rooted not only in an agency problem (or motor prediction error, see also Tsakiris et al. 2007a), but “may also reflect a disturbance in body ownership” (p. 513). Indeed studies using the rubber hand illusion paradigm suggest that schizophrenic patients show abnormal ownership experiences. These patients show an abnormally strong illusion with a much faster onset of the illusion (Peled, Pressman, Geva, & Modai, 2003; Peled, Ritsner, Hirschmann, Geva, & Modai, 2000; Thakkar, Nichols, McIntosh, & Park, 2011).

It seems that abnormal experiences in the rubber hand illusion might not be limited to clinically diagnosed schizophrenia. Abnormal experiences can be already observed at an earlier stage, when individuals might carry certain tendencies for delusional ideation (Germine, Benson, Cohen, & Hooker, 2012). Such tendencies for delusional beliefs might be not specific to a clinically manifest psychosis, but can be found as a trait also within the general healthy population (Peters, Joseph, & Garety, 1999; Peters, Joseph, Day, & Garety, 2004; Van Os, Linscott, Myin-Germeys, Delespaul, & Krabbendam, 2008). Crucially, individuals on the high end of this spectrum can be characterized by similar thought and perceptual processes as psychotic patients (Fusar-Poli et al., 2012; Schmack et al., 2013; Teufel, Kingdon, Ingram, Wolpert, & Fletcher, 2010). They also show higher risk for a clinically manifest psychotic disorder (Fusar-Poli et al., 2013). Therefore delusion-prone individuals might already show certain abnormal tendencies in the way they perceive their own movements. Given that these alterations do not manifest themselves in a pathological way, these changes in perception and cognition are rather subtle.

A way to quantify these tendencies however is the questionnaire of Peters and colleagues (Peters et al., 2004; 1999), which is an acknowledged screening inventory to test for the presence of delusion. It consists of 21 items that are rated for the presence of delusions and other factors like distress-level. By using this inventory it has been indeed shown that delusional tendencies are presence in the healthy population. It has also been shown that these ratings directly relate to performance levels in perceptual and motor tasks (Schmack et al., 2013; Teufel et al., 2010).

Other neurological syndromes like asomatognosia or anosognosia for hemiplegia are neurological disorders occurring often after stroke that affect more distinctly the sense of ownership or agency respectively. Asomatognosia reflects a syndrome in which patients believe that their limb is no longer part of their own body. This occurs often after lesions of the parieto-temporal or fronto-parietal cortex, but also insula cortex of the right hemisphere (Arzy, Overney, & Landis, 2006; Baier & Karnath, 2008; Feinberg & Haber, 1990). When the doctor holds up their hand in front of them, these patients deny that the hand they see is actually their own hand (Wortis & Dattner, 1942). In anosognosia for hemiplegia patients deny their hemiplegia. Thus despite the obvious deficit of being paralyzed these patients are not aware of their disorder. This is often seen after right hemisphere lesions involving fronto-parietal structures or other structures like the insula or thalamus (Berti et al., 2005; Gerstmann, 1942; Karnath, Baier, & Nägele, 2005; Orfei et al., 2007). It has been suggested that this disorder can be placed into the spectrum of agency related mechanisms, where the brain damage leads to a dysfunctional motor system. This makes the patient unable to accurately monitor their actions (Fotopoulou et al., 2008; Jenkinson & Fotopoulou, 2010).

Often the concepts of ownership and agency, and with this the syndromes of asomatognosia and anosognosia, are confused in the literature. This makes it difficult to infer the underlying mechanisms responsible for the pathology (Synofzik, Vosgerau, & Newen, 2008b). For example, Dieguez and colleagues (2007) "use the term asomatognosia as the general heading for the disorders of bodily awareness, where one´s body may be perceived in an unusual manner, or not perceived as having changed in its function". This definition seems to entail two different aspects: the former seems to relate to issues of asomatognosia (so, more ownership related) and the latter to anosognosia (so, more agency related) aspects. Partially this is rooted in the obvious problem that brain lesions after stroke usually damage wide cortical territories including the underlying white matter structure and can therefore lead to a variety of neurological symptoms co-occurring in the same patient (like neglect). In particular it has been shown that anosognosia is often confounded with a loss of ownership for the affected limb at the same time (Baier & Karnath, 2008; Feinberg & Roane, 2000).

4.3 A SHORT NOMENCLATURE

Before we continue it might be helpful to clarify the use of the terms of self-recognition, ownership and agency in the present thesis:
Bodily self-recognition is used here as a term to describe mechanisms, which enable us to identify our own body as something different than the environment. It refers the immediate and momentary feeling of perceiving the body as my body. In this way self-recognition is not only a question related to bodily awareness or consciousness, but becomes also a distinct perceptual problem. We do not include aspects related to the psychological self or to visual recognition like on pictures.

Bodily self-recognition entails ownership and agency as two different, but complementary aspects. Both can contribute to bodily self-recognition and can identify the body as one's own. Agency refers here to the sense of authorship, so the sense to be able to control and move the body voluntarily. Ownership refers to the experience of perceiving a body part as the own body part. Given this definition both these experiences represent different aspects of the movement, but they are often experienced in tight conjunction with each other. This poses a problem when experimentally probing these processes.

5 THE MOVING RUBBER HAND ILLUSION

The rubber hand illusion undoubtedly represents a major breakthrough in the investigation of the mechanisms underlying the perception of the own body (Botvinick, 2004; Botvinick & Cohen, 1998). However, as pointed out by Tsakiris and colleagues (2007b) the rubber hand illusion “lacks ecological validity, mainly because it does not involve bodily movement” (p. 650). The participant does not move during the experiment and the rubber hand always remains static. Therefore, the classical version lacks the dimension of action and agency. This is important, as we mainly perceive our own body during movements. We constantly use our body to walk, run, and reach for the things around us. This ability to control our body is a major source of information for the experience of the body. To fully understand the mechanisms of bodily self-recognition, in which both the sense of ownership for the body and the sense of agency over its movements take part, we need to be able to examine both these aspects more directly (S. Gallagher, 2000; Tsakiris & Haggard, 2005a; van den Bos & Jeannerod, 2002; Jeannerod, 2006),

A few studies directly investigated this question by inducing the illusion with movements instead. The first study has been conducted by Tsakiris and colleagues (2006). Participants experienced active movements, passive movements, and visuotactile stimulation while seeing a projected image of their own hand. Their hand was occluded from view and recorded with a video camera system. When measuring the proprioceptive drift they found no difference in the strength of the drift between the three conditions. However, they found a difference in how the feeling of drift spread over the rest of the hand. After active movements the proprioceptive drift spread across the hand and included other fingers (so, when the index finger moved and the little finger had to be localized). When the illusion was induced by passive movements or visuotactile stimulation, then the drift was restricted to the stimulated finger only, as if the drift stays localized. However, no subjective reports on the feeling of ownership and agency were collected in this study.

Dummer and colleagues (2009) used a different setup, in which not the individual fingers, but the whole hand is mechanically moved either in synchrony or asynchrony with respect to their own movement. They found a tendency for stronger illusion in the active movements than in passive movements, but the illusion in the active condition not to be stronger in the visuotactile condition. The experiment was based on questionnaire ratings regarding the sense of ownership, but not agency, and an objective measure was not applied (Dummer, Picot-Annand, Neal, & Moore, 2009) .

Longo and Haggard (2009) used a video screen based setup to test whether the feeling of ownership and / or agency would facilitate the reaction time to a visual stimulus given close to the hand. They tested active movements, passive movements and visuotactile stimulation. They found that reaction times were facilitated when ownership and agency were experienced. They also reported a main effect of induction type (i.e., the strength of the illusion differed in the three versions) (Longo & Haggard, 2009).

More recently Walsh and colleagues (2011) tested whether the illusion can still be induced under anaesthesia of the skin, thus removing certain sensory components normally stimulated in the illusion. Still in this situation without somatosensory feedback from the superficial skin the illusion can be induced. Surprisingly they found a stronger illusion in the passive movement condition, and also a stronger illusion in the anesthetized conditions than in the non - anesthetized conditions (Walsh, Moseley, Taylor, & Gandevia, 2011).

In sum, the literature of the rubber hand illusion induced by movements appears rather heterogeneous, making it difficult to conclude whether the illusion by movements differs to the classical version of this experiment or not. And if so, how it exactly differs. This is partly related to the differing procedures to induce the illusion (finger movements versus whole hand movements), the setup used (video-screen versus real hand) and differing approaches used to quantify the illusion (subjective reports and / or proprioceptive drift with differing measurement procedures). Partly these studies also aimed to answer slightly different questions, and were not primarily interested in the relationship of ownership and agency.

5.1 OBJECTIVES OF THE PRESENT WORK

The present work is motivated by the idea to develop a rubber hand illusion paradigm based on movements and with high ecological validity by using a real model hand.
This inclusion of movements allows a systematic investigation of ownership and agency within a single experiment. This will help us to understand the processes underlying the perception of ownership and agency and their individual contribution to the process of bodily self-recognition.

For this purpose we examined whether…

- … Movements can produce a strong ownership illusion and experience of agency in a rubber hand illusion paradigm.
- … The moving rubber hand illusion obeys similar perceptual rules as the classical illusion.
- … The moving rubber hand illusion differs from the classical illusion.
- …. The moving rubber hand illusion can be used as an experimental model to investigate psychiatric traits in relation to bodily self-recognition.

5.2 METHODS

5.2.1 The setup

The moving rubber hand consists of a wooden model hand (right hand) with movable finger joints that has the size of an average adult hand. The length is 20 cm (wrist – large finger tip) and width is 10 cm (thumb – little finger). The hand is placed on a wooden box with the measures of 20 x 30 x 12 cm. Therefore, the distance between the participant´s hand and the model hand is 12 cm, which is in the typical range of rubber hand illusion experiments. The model hand is covered with a latex glove. In the experiments the participant wore an identical glove on the right hand.

The box is placed on a table at a distance 50 cm from the participant, so that the participant can rest the whole forearm on the table. The participant´s right arm is covered with an opaque cloth to prevent sight of the own body (see Fig. 5-1). A light stick connected to plastic rings worn on the distal finger joint, and connected both the participant´s index finger and the model hand´s index finger.

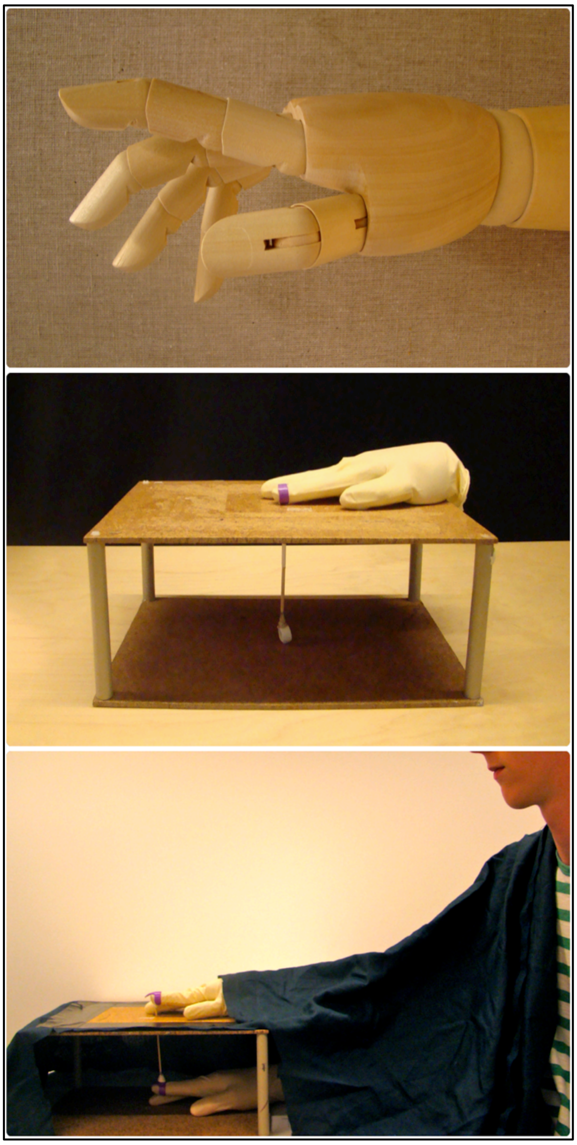

Figure 5-1: Illustration of the setup used in the experiments. A life-sized model hand is placed on a box. The participant places the arm on the table with the hand inside the box. The right arm is covered with an opaque cloth to prevent sight from the own body. This creates a perspective as if the model hand belongs the participant´s own outstretched arm.

As can be seen in Fig. 5.1, the model hand is placed on top of the box, thus above the participant´s hand. This vertical arrangement deviates from the initial setup introduced by Botvinick and Cohen (1998), in which both hands are place side by side in the horizontal plane, and which is the most common way used in rubber hand illusion studies. However, a number of studies have also used also this vertical arrangement and shown that also when placing the hands on top of each other the illusion can be reliably induced (Bekrater-Bodmann, Foell, Diers, & Flor, 2012; Ehrsson et al., 2004; Haggard & Jundi, 2009, Kammers et al., 2009).

5.2.2 Experimental procedure

In all experiments we used a procedure in which participants execute simple index finger taps (i.e., extension movement) at a rate of approximately 1Hz. Participants were trained to tap with a metronome before the experiment and instructed by the experimenter to execute the movements in the appropriate way. We decided not to use a metronome to pace the participant's movements during the actual experiment and instead let the participants move the finger freely. A concern here is that with a metronome participants might coordinate their movements with the external signal instead, which is known to evoke different neuro-cognitive processes (Jahanshahi, Jenkins, Brown, Marsden, Passingham, et al., 1995).

Participants were instructed to randomly introduce a "double-tap" (i.e., two rapid successive taps instead of a single tap). These double taps helped to control for habituation and also for alertness of the participants. Participants typically executed 3-5 double taps throughout a trial. Again, participants were instructed to make those double taps freely, without any external signal. Thus, these double taps were similarly self-paced. Each trial lasted typically between 90 and 120 sec. Participants had a break between each trial (between 30 – 45 sec) and were instructed to remove their hand out of the box and stretch and relax the right arm. These pauses help to prevent carry-over effects from one trial to the next. All trials were randomized and counterbalanced to control for order effects.

Throughout our experiments we applied various manipulations: we varied the **timing of the feedback** (Synchronous versus Asynchronous), **the mode of movement** (Active versus Passive) and **the position of the model hand** (Congruent versus 180° rotated):

Timing: A widely used manipulation is the timing. During *synchronous movement* the model hand´s finger moves in synchrony with the participant´s finger. In *asynchronous movements* the model hand´s finger is disconnected from the participant´s finger and is moved by the experimenter with a delay. When we use the term "asynchronous", we strictly use it a temporal manner. This means that the model hand finger moves approximately 500 ms after the participant´s hand and both events do not coincide at any given moment in time. Crucially, this stimulation procedure ensures that the number of sensory events is equal in each condition (i.e., same number of fingers taps and visually observed finger taps).

Mode: During *active movements* the participant executes the finger movement by him or herself. In *passive movements* the experimenter moved the connecting stick while the participant remained passive and did not actively participate in the generation of the movement. The experimenter here mimicked the finger movements of the participant by observing the participant in the training phase, so making the passive finger movement similar in terms of amplitude or movement speed.

Position: The position of the model hand can be changed. Typically the hand lays in a posture *congruent* to the participant´s outstretched arm on the table, thus in an anatomically plausible position. We also placed the rubber hand in an incongruent position, where we rotated the model hand to a *180°*. This rotation induces a mismatch between the visually observed (model) hand and felt position of the (participant´s) hand; see Fig. 5.2.

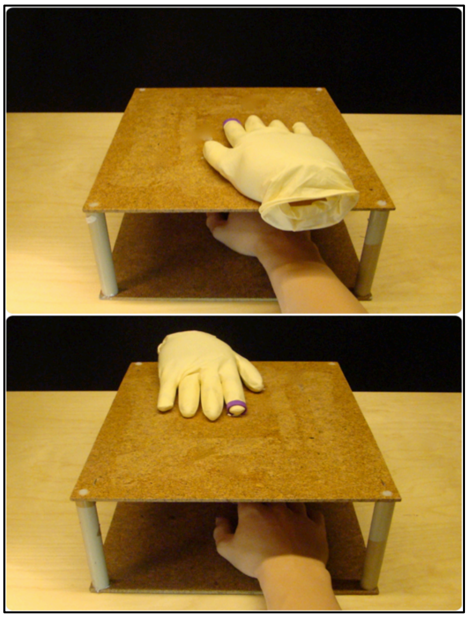

Figure 5-2: The model hand can be placed in an anatomically plausible position (upper) or a 180° rotated (lower). Note that the cloth covering the right arm is removed here for illustration purposes.

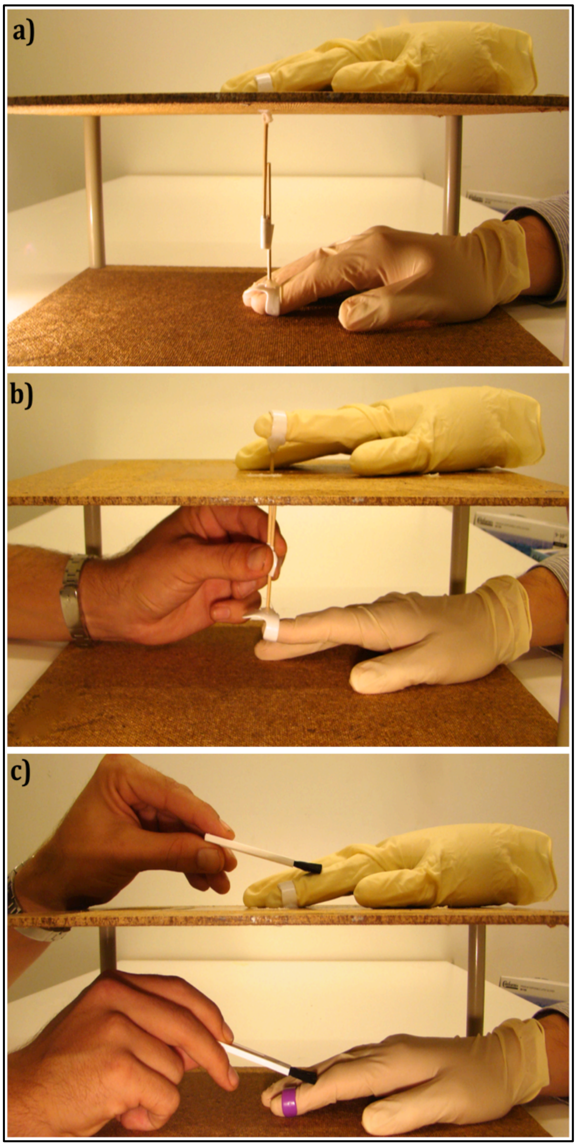

Figure 5-3: The three different ways to induce the illusion:

a) Active movements: The participant makes simple index finger taps.

b) Passive movements: The experimenter moves both the model hand´s and participant´s index finger with the connecting stick.

c) Visuotactile stimulation: The experimenter applies brush strokes on both index fingers. No movement is present here.

In experiments in which we compared the moving rubber hand illusion to the classical illusion (Study II and III) we carefully adopted the procedure described above for the visuotactile stimulation. Instead of the finger tap we applied a **tactile stimulus** by using a small brush to both the participant´s and model hand´s index finger at a rate of 1Hz, which is done either synchronously or asynchronously. During asynchronous stimulation the model hand´s finger is touched after the participant´s finger is touched. This is similar to the movement condition in which the participant moves first and then the model hand moves. Also here we introduced some double stimulation (i.e., "double strokes") as the equivalent to the "double taps" in the moving rubber hand illusion. With this procedure we aimed to keep the temporal characteristics of the stimulation and number of sensory events equal across induction types. When I use the term "induction type" in the following, I refer to the three different ways of inducing the illusion: active movements, passive movement and visuotactile stimulation (= classical version of the rubber hand illusion), see Fig. 5-3.

5.2.3 Measuring the experience of the illusion

5.2.3.1 A subjective measure: Questionnaire

In our questionnaire assessment we always used multiple statements reflecting the experience of ownership (e.g., "*I felt the rubber hand was my own hand*") and agency (e.g., "*I felt as if I control the movement of the rubber hand*"). Participants rated these on a 7-point Likert scale ranging from -3 to +3, where 0 indicates uncertainty.

We then averaged these ratings to an overall ownership or agency rating score. At the same time we also included control statements for both ratings, which did not reflect the experience of ownership and agency (e.g., "*I felt as if my right hand disappeared*" or "*I felt as if the rubber hand a will of its own*"). These statements control for overall task compliance and unspecific responses. Statements were adopted from previous experiments and modified (Botvinick & Cohen, 1998; Longo et al., 2008).

Questionnaire items [1]

Ownership: Statements in this category reflect the experience of perceiving the model hand as part of the own body, thus reflecting the sense of ownership.

1. *I felt as if I was looking at my own hand*
2. *I felt as if the rubber hand was part of my body*
3. *It seemed as if I were sensing the movement of my finger in the location where the rubber finger moved*
4. *I felt as if the rubber hand was my hand*

Many studies on the classical illusion use the referral of touch statement, which refers to when the participant perceives the tactile stimulus at the place where the model is touched. This statement is often highly rated during the illusion. We excluded this statement from our questionnaire, as no external stimulation is present in the moving rubber hand illusion.

[1] Please refer to the studies to see the statements used in each individual experiment

Ownership Control: These statements reflect a possible somatic sensation of the model hand or real hand, which are unrelated to the experience of ownership of the model hand.

1. *I felt as if my real hand were turning rubbery*
2. *It seems as if I had more than one right hand*
3. *It appeared as if the rubber hand were drifting towards my real hand*
4. *It felt as if I had no longer a right hand, as if my right hand had disappeared*

Agency: The agency statements reflect the sense of being the author of the model hand´s movements, thus being able to exert control over the hand or being able to cause the hand to move.

1. *The rubber hand moved just like I wanted it to, as if it was obeying my will*
2. *I felt as if I was controlling the movements of the rubber hand*
3. *I felt as if I was causing the movement I saw*
4. *Whenever I moved my finger I expected the rubber finger to move in the same way*

Because in some experiments (Study II and III) we directly compare the moving rubber hand illusion to the classical illusion (in which no movement occurs), we reformulated the agency statements. These statements were formulated in a way as if the participants *could* be able to move the hand if they wanted to do so, see also Longo et al. (2008). This differs from the experience of an executed movement, and therefore is more an indirect measure of agency.

1. *I felt as if I could cause movements of the rubber hand*
2. *I felt as if I could control movements of the rubber hand*
3. *The rubber hand was obeying my will and I can make it move just like I want it*

Agency Control: Statements in this category reflect an experience of will or causation, but not in a way where the participant feels being in control over the model hand.

1. *I felt as if the rubber hand was controlling my will*
2. *I felt as if the rubber hand was controlling my movements*
3. *I could sense the movement from somewhere between my real hand and the rubber hand*
4. *It seemed as if the rubber hand had a will of its own*

We analysed the questionnaire ratings according the following logic in order conclude that participants report a clear experience of ownership and agency:

1) The **median group rating should be equal or higher than +1**, which requires that the majority of participants give a clear positive rating.
2) Within the condition the ownership or agency rating should be **significantly different to its control rating** (e.g., Ownership versus Ownership Control rating in synchronous movements).
3) The **control rating should not be affirmed,** thus participants should not positively rate these unrelated statements.
4) The ownership or agency rating should be **significantly different to the same rating of a control condition** (e.g., Ownership rating Synchronous vs. Ownership rating Asynchronous).

To compare the ratings across conditions we use a Wilcoxon test for pairwise comparison and a Friedmann test for multiple comparisons.

As an additional measure we used the cut-off score of +1 to categorise participants into responders (i.e., illusion) and non-responders (i.e., no illusion), and we compare the number of responders across conditions. With responder we mean a participant who gave high affirmative ratings of ownership or agency ($\geq +1$). This is motivated by the following objective. When we observe a significant difference in the ownership ratings between two conditions, then this could be rooted in two different reasons:

1. There is a true difference between the strength of the ownership experience of the two conditions or
2. The number of ownership responders (i.e., participants who in principal are responsive to the illusion) is just lower, so which can in turn lead to lower average rating in this condition.

Thus, the difference might not necessarily be a true difference in the strength of the rating of the participants experiencing the illusion, but in the overall number of participants responding to the illusion per se (given we have to assume that a proportion of participants will not experience the illusion per se). To disentangle both these possibilities we use both these statistical comparisons (i.e., the absolute ratings and the number of responders) to examine the potential differences between the conditions. This additional analysis can give some further insight into the specific differences observed. In sum, we aim to ensure a specific assessment of the questionnaire to evaluate the experience of ownership and agency in our participants.

5.2.3.2 An objective measure: Proprioceptive drift

We used a proprioceptive drift task as an objective and complementary measure of the illusion (Botvinick & Cohen, 1998; Tsakiris et al., 2006; Tsakiris & Haggard, 2005b). It consists of a pointing procedure in which the participant has to indicate the perceived position of the right (stimulated) hand, with the eyes closed. Participants pointed with the left (unstimulated) index finger on a board with a millimetre grid, mounted on the left side of the box (see Fig. 5-4). As such pointing movements can exhibit a certain degree of variability we use multiple repetitions (i.e., three repetitions per condition) and average the three values. We then compare the drift values in the different conditions (e.g., synchronous versus asynchronous feedback). The data was tested for normality with a Shapiro-Wilk test and the appropriate parametrical or non-parametrical tests have been used.

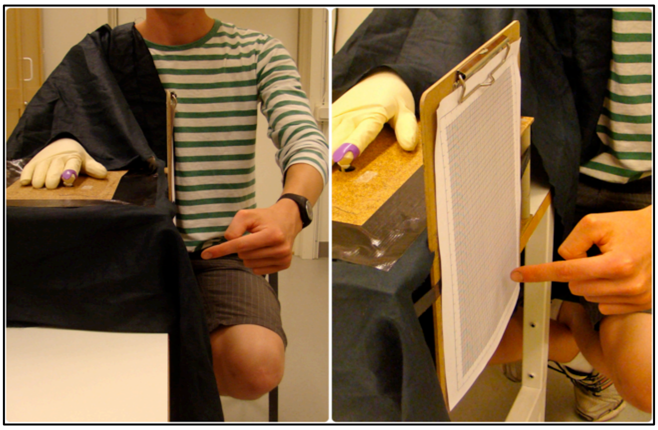

Figure 5-4: Illustration of the setup used in the proprioceptive drift experiments. Participants pointed to the felt position of the right hand with their left index finger.

We obtain two measurements per trial: a pre- and post – pointing value, which are subtracted from each other to derive a single value (**Post minus Pre**). A positive value represents a drift upwards (i.e., towards the rubber hand). This positive drift indicates that the participants perceived their real hand to be closer to the model hand. This procedure differs from other approaches to measure the proprioceptive drift, which use perceptual position judgments instead of a pointing movement (Riemer et al., 2013; Tsakiris et al., 2006).

5.3 SHORT SUMMARY OF THE STUDIES

Study I

In the first study we tested 104 naïve participants in four different experiments. We aimed to validate the setup (Exp.1 and 2) by comparing the effect of synchronous and asynchronous feedback on the subjective experience (Exp.1, n = 20) and proprioceptive drift (Exp. 2, n = 20). Subsequently we tested the effect of different manipulations on the experience of ownership and agency (Exp. 3 and 4). We varied the mode of the movement (active versus passive) and position of the model hand (congruent versus rotated) and examined the subjective experience (Exp. 3, n = 32) and the proprioceptive drift (Exp. 4, n = 32).

Study II

In study II we tested 60 naïve participants and directly compared active movements, passive movements and visuotactile stimulation as different ways to induce the illusion of ownership. We examined the subjective experience of ownership and agency in all three induction types with synchronous and asynchronous stimulation (Exp. 1, n = 40). In Experiment 2 (n = 20) we compared active movements with visuotactile stimulation by using the proprioceptive drift.

Study III

In the third study we examined the effect of distance between the hands in 60 naïve participants. We compared the moving (active movements) and classical rubber hand illusion at three different distances between the model hand and the hand of the participant. In Experiment 1 we tested 40 participants with synchronous and asynchronous stimulation at the three distances of 12 cm, 27.5 cm, and 43 cm. In Experiment 2 (n = 20) we tested the moving rubber hand illusion at the distance of 12 and 27.5 cm using the proprioceptive drift test.

Study IV

In the fourth study we explored the potential link of the experience of ownership and agency in the moving rubber hand illusion to traits of delusions in a healthy group of participants. 72 naïve participants experienced active and passive movements (with synchronous or asynchronous feedback). We used the Peter´s delusion inventory (PDI) to assess the presence of delusional believes, which serves as an indicator for tendencies of psychotic traits. We examined potential links between unusual tendencies in the ownership and agency experience (as measures for bodily self-recognition) in the moving rubber hand illusion and delusional traits as measured by the PDI scores for each individual.

6 RESULTS

6.1.1 Inducing the illusion with movements

After active synchronous movements participants gave high ratings of ownership (Median in Study I = 2.0, Study II = 1.7, Study III = 1.7, Study VI = 2.0)[2]. Thus, observing a model hand that moves in synchrony with the participant´s own movement evokes a strong illusion of ownership towards the model hand (see Fig. 6.1). When the feedback was asynchronous (Study I, II, III and IV) or the model hand was rotated to a 180° (Study I), the ownership ratings were always negatively rated. Similarly, the ownership control ratings were negatively rated in all studies.

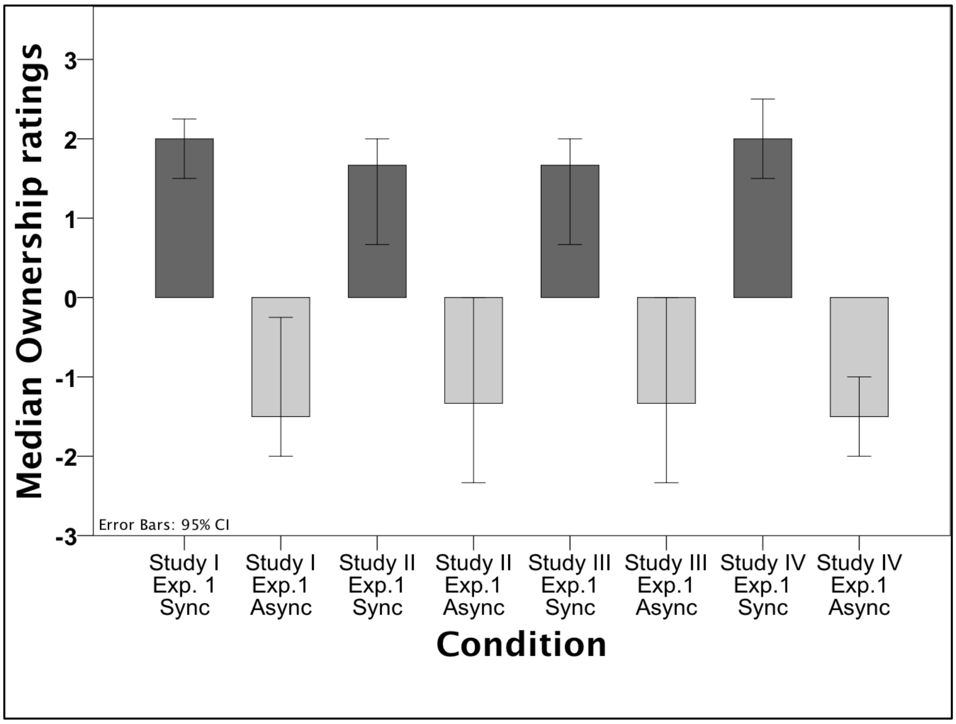

Figure 6-1: Ownership ratings of the synchronous (dark) versus asynchronous (light) active conditions of the four studies. A strong experience of ownership has been always reported in the synchronous conditions.

When we classify the participants as illusion responders by using a cut-off score of +1, we see that the majority of participants experience a strong illusion. Across studies about 72% (ranging from 63 – 86%) of our participants experienced a sense of

[2] Please note that the values of Study I differ here from the figures in the publication (Kalckert and Ehrsson, 2012), in which the mean values are shown. Here, we use the median, as in all subsequent studies to show the data.

ownership in the synchronous conditions (see Table 1). This is in line with other reports reporting that about 60 to 80% of the participants experience an illusion (Ehrsson et al., 2004; 2005; Lloyd, 2007).

	Study I	Study II	Study III	Study IV
Percentage	**75 %**	**63%**	**65%**	**86%**

Table 1: Table showing the percentage of illusion responders (ownership rating of ≥ +1) in the synchronous conditions: Study I, Exp.1; Study II, Exp. 1; Study III, Exp. 1; Study IV.

In the moving rubber hand the illusion can be a result of active or passive movements. In Study I, II, and IV we tested active and passive movements. Passively experienced movements can trigger an ownership illusion just as active movements. Also during passive movements a proprioceptive drift of similar magnitude can be observed (Study I, Exp. 4). Therefore, we can conclude that efferent signals are not necessary to induce the illusion, as in passive movements also the match between the visually observed finger and the (passively) felt movement is sufficient to induce the illusion. However, it seems that active movement result in slightly higher ratings than passive movement (Fig. 6-2). In study I and IV we observed here a significant difference between active and passive movement condition, but not in Study II. For further discussion whether the illusion differs between active and passive movement, see Section 6.1.4.

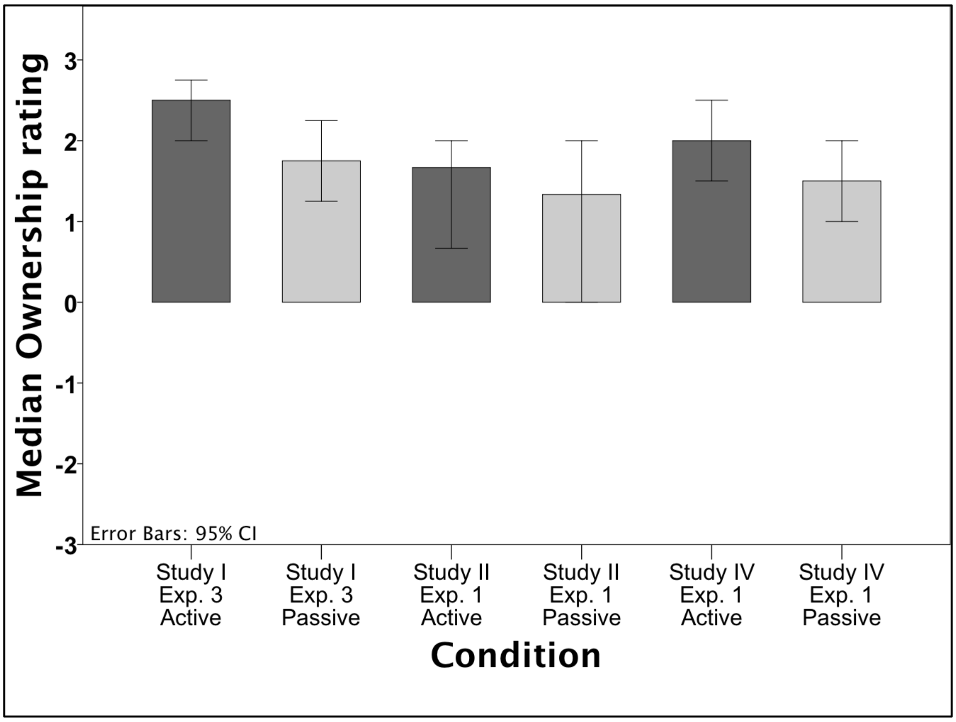

Figure 6-2: Ownership ratings in the active (dark) versus passive (light) conditions in the three studies in which we directly compared active and passive movements.

In sum, our experiments consistently show that the present setup is able to reliably evoke the illusion by movements without any external visuotactile stimulation. Both active and passive movement induce an experience of ownership.

6.1.2 Manipulating the ownership experience

We explored the perceptual rules of the moving rubber hand illusion and found them to be similar to observations in the classical rubber hand illusion. We found similar to the classical illusion that the temporal rule, spatial rule and anatomical plausibility rule apply to the moving rubber hand illusion.

Temporal rule: Asynchronous stimulation effectively cancels out the ownership illusion. In all experiments we included asynchronous movements as a control condition. Indeed, in asynchronous movements the majority of participants did not experience the illusions as indicated by the negative ratings in all our experiments; see Fig. 6-1.

Spatial rule: Studies have shown that the two hands must be sufficiently close in space to induce the illusion (Lloyd, 2007; Preston, 2013). In Study III we varied the distance between the two hands (ranging from 12 to 43 cm). We also saw that there is a spatial limit to the illusion in the moving rubber hand, similar to the classical version. Thus with increasing distance the illusion of ownership is abolished. Already at a distance of 27 cm significantly fewer participants experienced the illusion (Median = 0,3), which suggests a narrower spatial window than the classical rubber hand illusion.

Anatomical plausibility: A critical factor is the anatomical plausibility of the hand, thus the relative position of the rubber hand with respect to the participant's arm (Ehrsson et al., 2004; Ide, 2013; Tsakiris & Haggard, 2005b). In Study I we rotated the model hand to an anatomical implausible position (i.e., 180° rotated), which effectively eliminated the illusion of ownership. This was confirmed by both the subjective ratings (Exp. 3) and a lack of proprioceptive drift (Exp. 4).

6.1.3 Manipulating the agency experience

In all experiments we not only examined the experience of ownership, but also the experience of agency. Whenever the model hand´s finger moved synchronously with the active finger movements of the participants, a strong sensation of agency over the observed finger movements was reported (Median in Study I = 2.5, Study II = 2.7, Study III = 2.7, Study VI = 3.0). The agency ratings were reduced during asynchronous feedback, but never clearly denied in the active conditions (see Fig. 6-3).

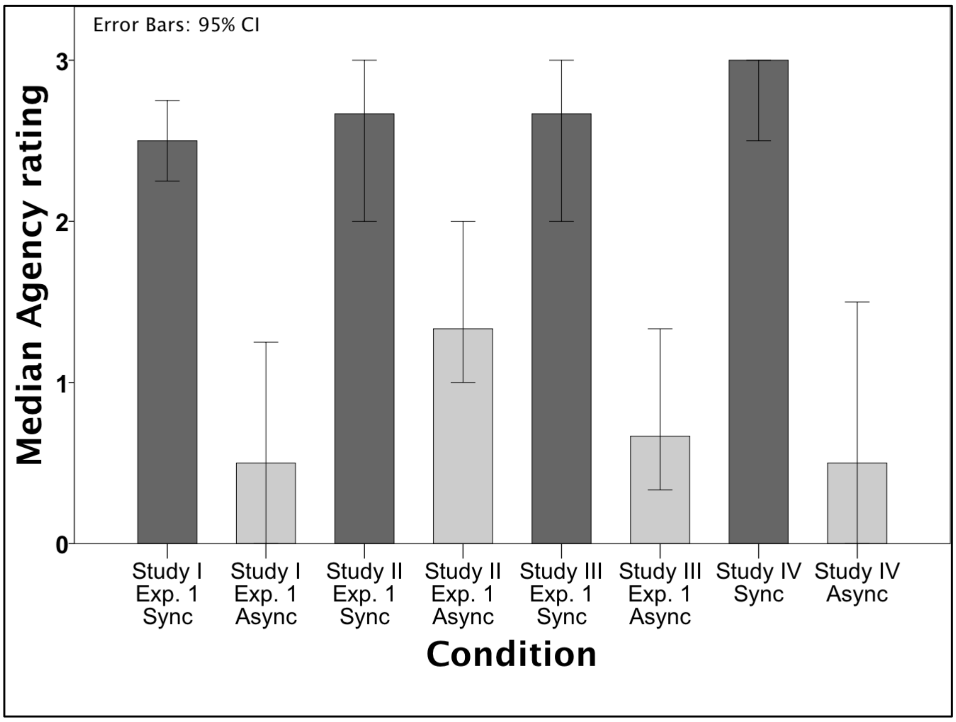

Figure 6-3: Agency ratings in the synchronous (dark) versus asynchronous active

conditions (light) in all four studies. Asynchronous feedback significantly reduces agency, but does not lead to a complete negation of agency.

Also during passive movements participants did not experience agency (Median in Study I = -0.7, Study II = 0.0, Study VI = -0.5). As can be seen in Fig. 6-4 agency ratings tended to be negatively rated in passive movement conditions.

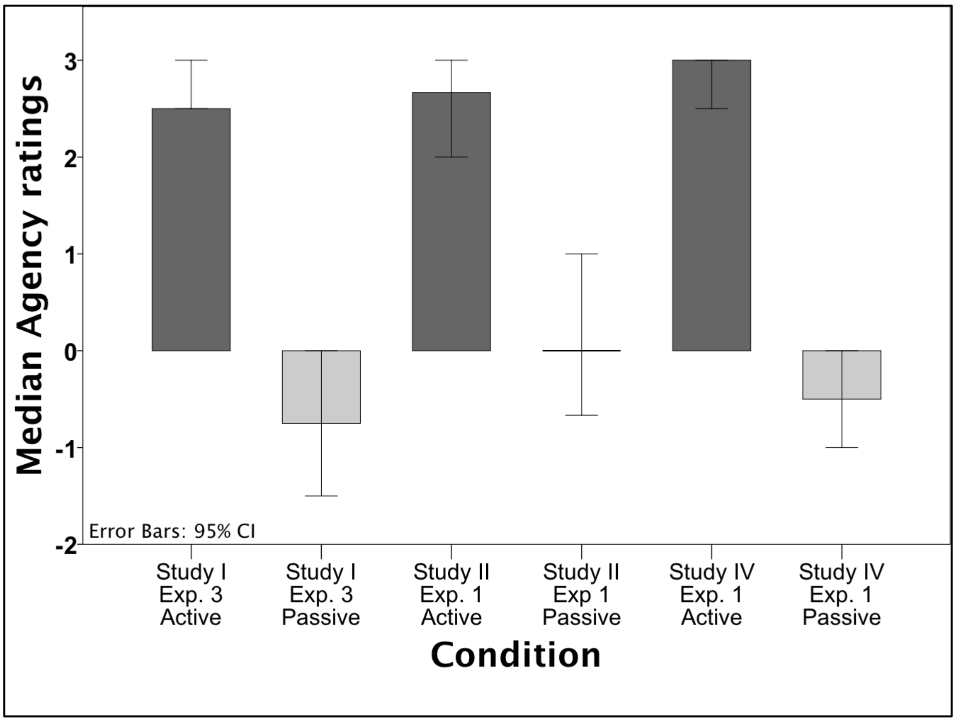

Figure 6-4: Agency ratings in the active (dark) and passive (light) synchronous conditions, agency is significantly affected by the mode of movement generation.

As both passive movement and asynchrony can influence the experience of agency, we can ask which of these two manipulations is actually more potent to reduce agency (Study I and II). In Study I we could only make this comparison between groups and found that the agency rating was significantly higher in the asynchronous condition (Exp. 1) than in the passive conditions (Exp. 3). We replicated this finding in Study II with a within-group comparison and found again higher agency ratings in the asynchronous condition as well ($Z = -2.492$, $p = .01$; not reported in Study II). Thus, passive movements lead to significantly lower agency ratings than asynchronous feedback.

6.1.4 Manipulating the sense of ownership and agency

The three manipulations we applied (Timing, Mode, Position) differently affected the experience of ownership and agency.

Timing: the timing of the feedback affects both ownership and agency, thus when the model hand moves asynchronously participants do not experience neither ownership nor agency (see Study I, II, III and IV).

Mode: when participants experienced passive movements, then they did not report an experience of agency. However, ownership can still be experienced, irrespective if the hand moves actively or passively (Study I, Exp. 3; Study II, Exp. 1).

Position: when the model hand was rotated to a 180°, then participants did not experience ownership. In contrast, a sense of agency can still be experienced (see Study I, Exp. 3). Thus, the position of the model hand did not directly affect the experience of agency, but affected ownership.

Taken together, these results suggest that ownership and agency obey different perceptual rules. Whereas timing affects both ownership and agency, the mode primarily affected the agency experience and the position the ownership experience.
Therefore, when combining the above-mentioned manipulations it should be possible to affect either ownership or agency in isolation. In Study I (Exp. 3 and 4) we demonstrate that both ownership and agency can be directly targeted by the appropriate combination of manipulations (see Fig. 6-5). In these experiments we applied two manipulations: mode of movements (i.e., active versus passive), and anatomically plausibility (i.e., congruent posture versus 180° rotated position). In active congruent movement participants experienced a sense of ownership and agency at the same time. In passive congruent movements agency was not experienced, but a sense of ownership was still present. When the hand rotated to a 180°, then during active movements participants experienced a sense of agency, but not during passive movements (Exp. 3).

This was supported by the drift experiment. A drift was present in the two congruent conditions in which participants experienced ownership. This was not the case for the two incongruent conditions in which ownership was not experienced (Exp. 4). In conclusion, this observation demonstrates a dissociation of ownership and agency.

Further support for this claim can be drawn from Study III: when we increased the distance between the two hands, we observed a reduction in the ownership sensation with increasing distance, thus at further distances participants do not experience ownership. However, participants still experience a sense of agency over the perceived finger movements, also at the furthest distance of 43 cm. Thus, the spatial rule applies to ownership, but not agency.

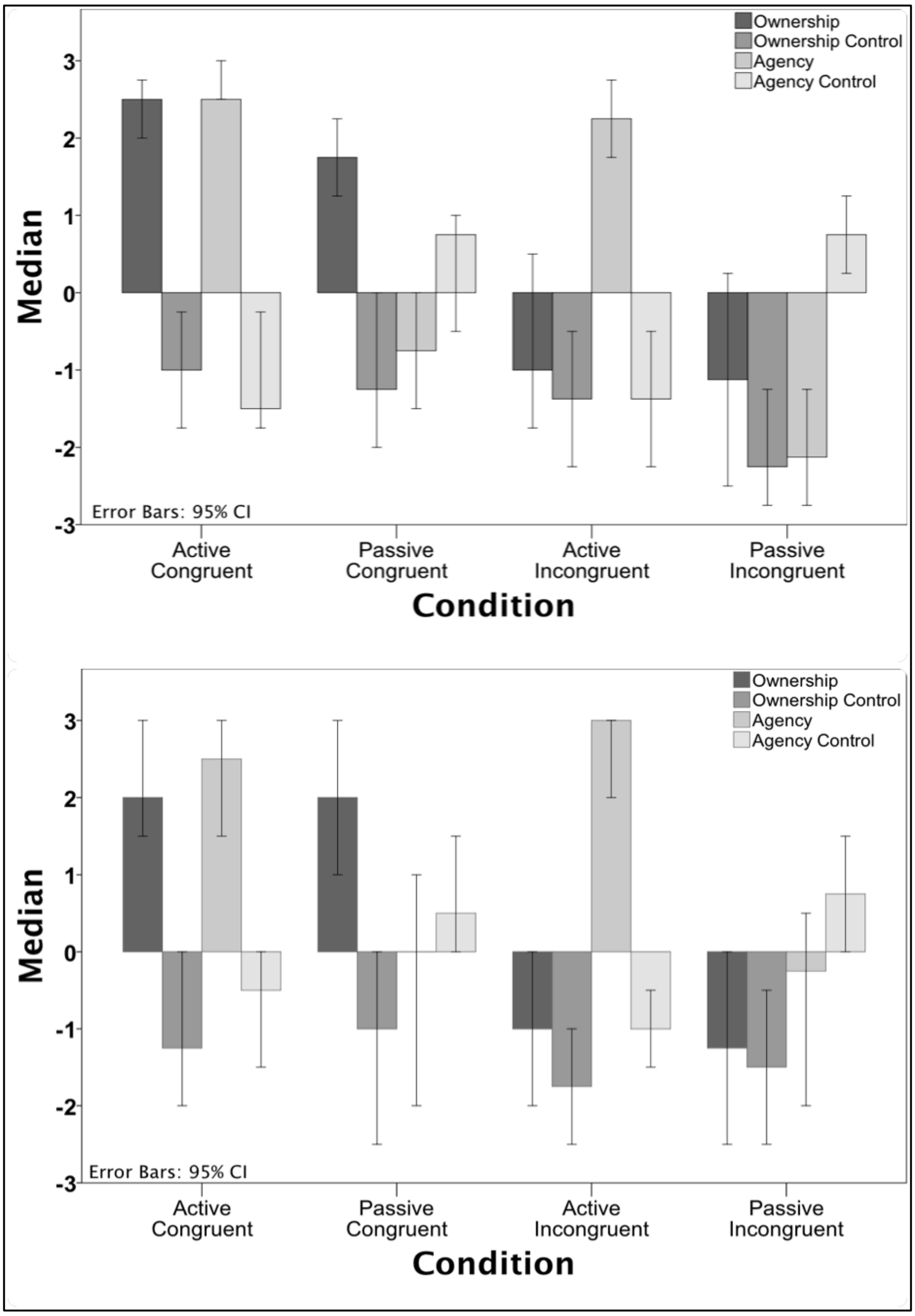

Figure 6-5: Results showing the dissociation of ownership and agency. Upper graph shows the original result in Study I, Exp. 3. The lower graph shows a replication of this result in Exp. 4 (not shown in Kalckert and Ehrsson, 2012).

6.1.5 Interaction of ownership and agency

A crucial question is whether and if so, how ownership and agency influence each other. A good starting point to answer this question is to compare the individual ratings across conditions and examine if the ownership ratings are higher during active than in passive movements. This would suggest that active movements lead to a stronger ownership illusion. Our results across studies are mixed in this regard: in study I we found that the overall ratings in active movements were higher than in passive movements. The number of responders however was not statistically different though, from which we can conclude that active movements do not result in a higher number of responders. Those participants who experience the illusion gave slightly higher ratings (Exp. 3). The drift data however indicated no significant difference between active and passive movements (Exp. 4). Therefore we could not confidently conclude that active movements lead to a stronger ownership illusion. Also in Study IV we saw higher ownership ratings in active movements. In study II however, where we directly compared the different induction types, we did not find a significant difference between active and passive movements: neither in the ratings nor in the number of responders. Active movements also did not lead to a stronger drift than in the classical illusion using visuotactile stimulation (Study II, Exp. 2).

Another way to address the issue under discussion is to look for correlations between the ownership and agency ratings. In Study I and II we indeed found correlations between ownership and agency. These were observed only in those conditions in which the hand moved synchronously and the model hand was placed in a congruent position. When the model hand was rotated, then this correlation was not present (Study I, Exp. 3). This suggests that this interaction between ownership and agency is not present in all situations.

In Study I (Exp. 3) we performed an interaction like analysis to further elucidate this seemingly complex relationship between ownership and agency. In this analysis we asked whether ownership ratings are always higher in active movements than in passive movements, irrespective of the position of the model hand. To this end we computed a difference-score between the congruent and rotated conditions for both active and passive movements. This difference was not significant, therefore suggesting that in active movements ownership ratings are not per se higher than in passive movements.

Likewise, we performed this kind of interaction analysis for the agency ratings: here we asked the question whether the position of the model hand affects the agency ratings, while keeping in mind that the two congruent conditions are conditions in which participants experience ownership. Thus, we ask whether in the ownership conditions the agency ratings are higher than in non-ownership (i.e., rotated) condition. This difference approached significance ($p = .06$), which perhaps suggests that agency ratings tend to be higher in the context of ownership. In Study II (Exp. 1) we found further, albeit more indirect, support for this conclusion: in the passive and visuotactile conditions the agency ratings increased during synchronous stimulation, as compared to asynchronous stimulations. In fact, one could expect that in the passive conditions it should not make a difference whether the feedback is synchronous or asynchronous. In these conditions no movement intention is formed, whose prediction could be violated by the asynchronous feedback. Still the agency ratings increased, which might suggest that a sense of ownership results also in a slight increase of agency. Taken together, these observations suggest that ownership might enhance the experience of agency, but that agency does not facilitate ownership per se.

6.1.6 The classical and moving rubber hand illusion

In study II and III we not only tested the moving rubber hand illusion, but also directly compared it the classical rubber hand illusion in the same group of participants.
Both the moving and the classical rubber hand illusion obey very similar perceptual rules. For example, similar to the classical version the moving rubber hand illusion is abolished after asynchronous stimulation or rotation of the model hand (Study I, Exp. 3 and 4).

After synchronous visuotactile stimulation or synchronous movements participants positively rated the ownership statements. The median ratings across studies were identical and let us conclude that the illusion in the moving rubber hand illusion is as strong as in the classical version; see Fig. 6-6.

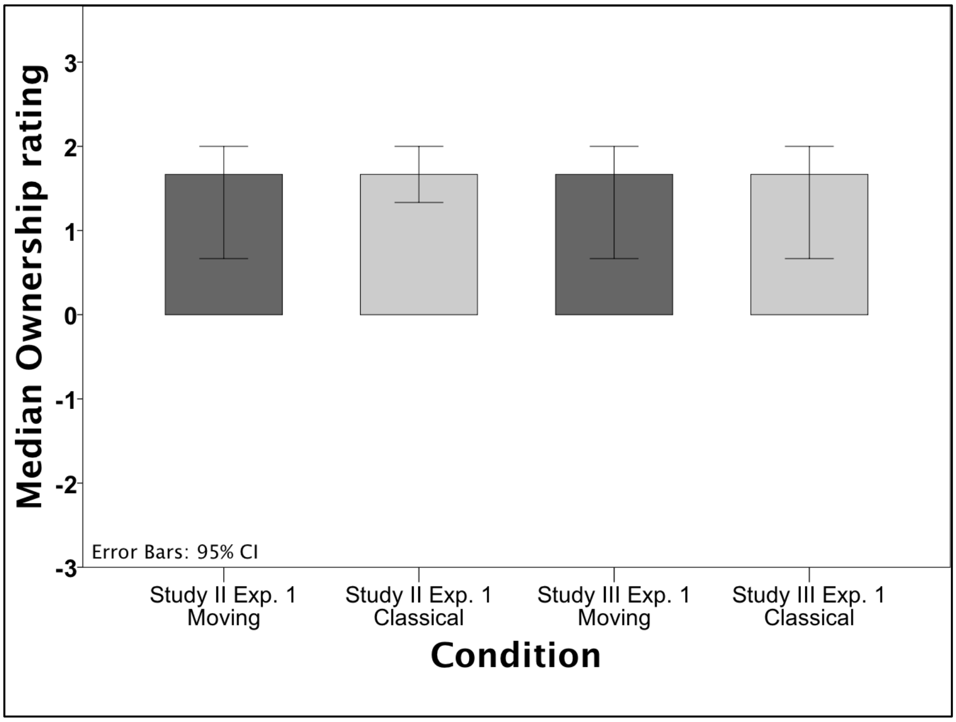

Figure 6-6: Ownership ratings of the synchronous conditions of the moving and classical rubber hand illusion in direct comparison. Both versions lead to strong experience of ownership, even of equal strength.

Also the number of illusion responders is very similar across induction types, therefore the specific way of inducing the illusion is not critical (although some interindividual differences were noticed, see Study II).

Moreover, the ownership ratings were highly correlated between induction types. In Study II we directly compared the three different induction types and examined whether the ownership ratings correlate between the different synchronous conditions, in which an illusion was present. Indeed we found a high correlation between active movements, passive movement, and visuotactile stimulation. In study III (Exp. 1) we similarly observed a high correlation between the ownership ratings between active movements and visuotactile stimulation (at the closest distance). This supports the idea of similar mechanisms involved in the different versions of the illusion.

Besides this general agreement, we noticed indications for a difference between moving and classical illusion in study III. When we varied the distance between the participant´s hand and model hand we saw that both induction types exhibit a spatial limit. Thus, with increasing distance the illusion is substantially diminished. The moving rubber hand illusion appears to follow a somewhat narrower spatial rule.

Whereas in the classical illusion participants still affirm ownership at the 27 cm distance, this was not the case for the moving rubber hand illusion. At this distance of 27 cm the absolute ratings were significantly lower than at the 12 cm distance and no significant proprioceptive drift between synchronous and asynchronous condition was observed. This observation merits further investigation and might represent the only noticeable dissimilarity we have seen in our experiments so far when comparing moving and classical rubber hand illusion.

Taken together, our results suggest that both versions are strongly related to each other and draw upon similar processes in the ownership illusion. However, agency is only clearly experienced in the moving rubber hand illusion, when participants voluntary move the finger and get synchronous feedback.

6.1.7 The proprioceptive drift as an objective measure

In Study I, II and III we measured the proprioceptive drift as an additional objective measure. We repeatedly found that during the illusion participants show a drift towards the model hand (as a significant difference between the drift in the synchronous versus asynchronous condition; see Study I, Exp. 2 and 4; Study II, Exp. 2 and Study III, Exp. 2). Thus a drift was present in conditions in which participants experienced ownership of the hand, irrespective of induction type.

We also correlated the drift with the subjective ratings to test whether participants with a particular strong illusion also show a stronger drift in the same conditions. Indeed this was the case, as reported in previous studies (Botvinick & Cohen, 1998; Longo et al., 2008). As in synchronous con ditions participants not only experience ownership, but also agency, we also correlated the drift measure with agency ratings. Here we did not find a significant correlation between drift and agency ratings (see Study I, Exp. 2; Study II, Exp. 2). Similarly we did not observe a drift in the active incongruent condition in Study I (Exp. 4), when participants feel only agency, but not ownership. Therefore we conclude that the proprioceptive drift is a measure of the ownership experience. So, only during the ownership illusion a relocation of the felt position of the own hand towards the rubber hand can be observed, but not during the experience of agency; see Fig. 6-7.

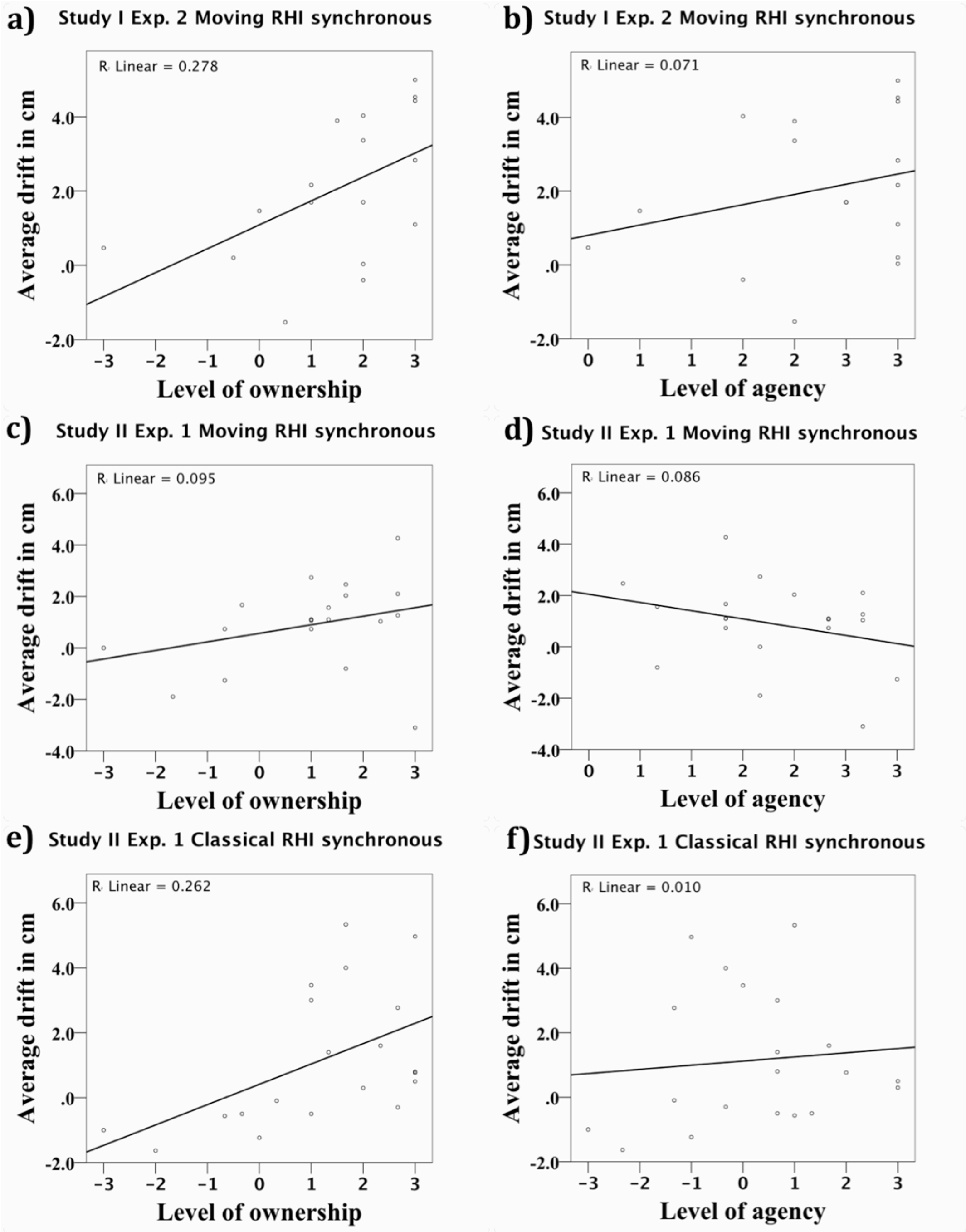

Figure 6-7: Correlations between the proprioceptive drift and the subjective ratings of ownership and agency. The drift is correlated to the ownership ratings, but not agency

6.1.8 Bodily self-recognition and delusion proneness

In Study IV we examined the relationship between ratings of ownership and agency as measures of self-recognition and delusion proneness. We found that individuals on the high end of the spectrum reveal tendencies for an increased sense of agency in passive movements, whereas active movements are perceived essentially in the same way by participants with high – or low delusional tendencies. Besides this specific observation, which was dependent on the fact of whether participants moved actively or passively, an overall general increase of ownership ratings across conditions with increasing delusion proneness was observed too. This suggests that delusion-prone participants exhibit an atypical experience in the moving rubber hand illusion; see Fig. 6-8.

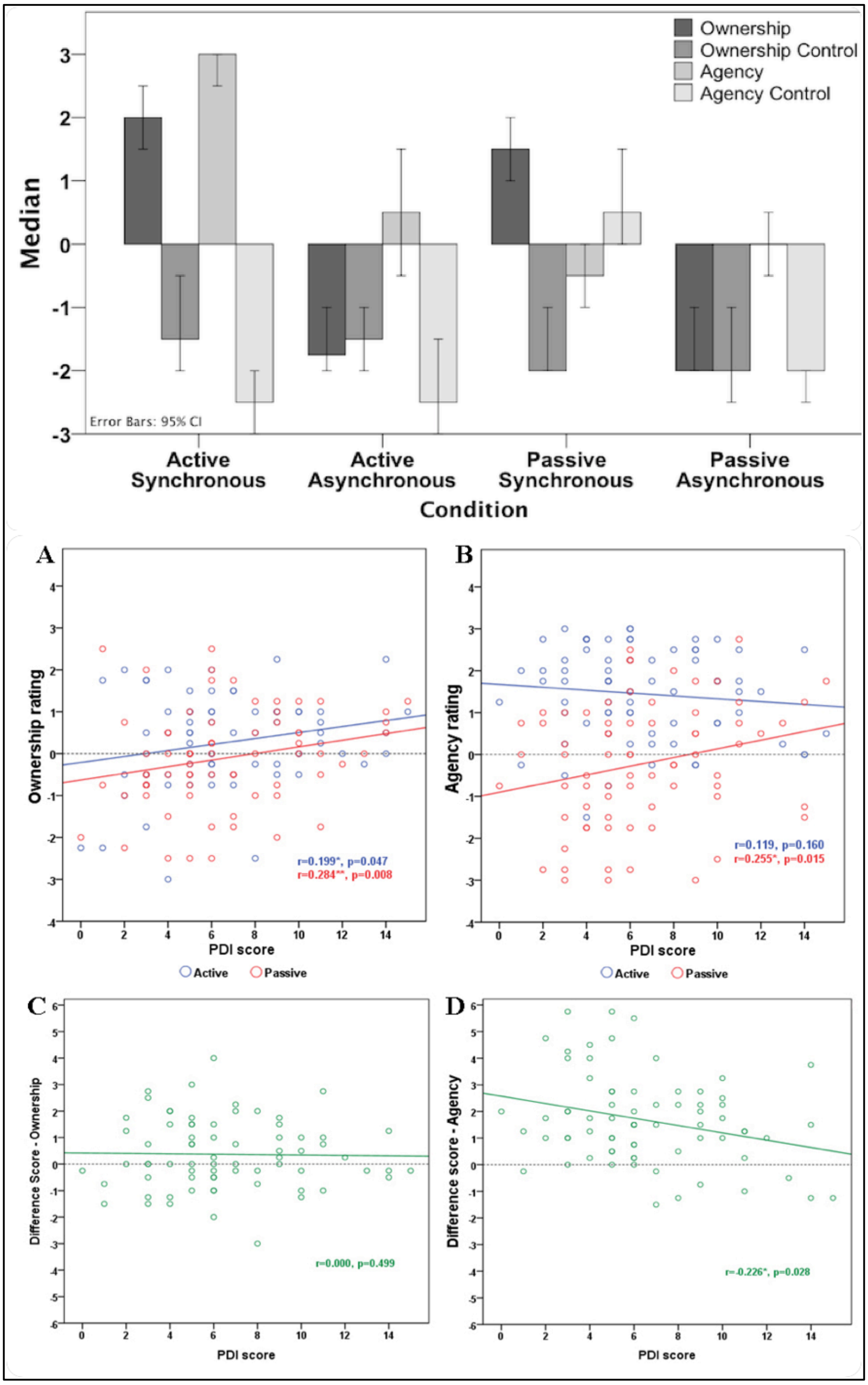

Figure 6-8: Results of the questionnaire in study IV (upper). Lower graphs show correlations to the PDI scores when active versus passive movements are compared.

6.1.9 Further observations

6.1.9.1 The effect of handedness

In Study II we measured the laterality by using the Edinburgh Inventory for handedness (Oldfield, 1971). In Exp. 1 the average laterality (LQ) was 69.7 (SD 42.5, range: -73.3 to 100). We correlated the LQ using a Spearman rank correlation to the ownership category to the synchronous condition of active movements, passive movements, and visuotactile stimulation to check if the strength of the illusion is influenced by the handedness. We did not find a significant correlation between the handedness and ownership rating in the active movements condition ($r = 0.213$, $n = 40$, $p = .186$), passive movements condition ($r = 0.008$, $n = 40$, $p = .959$) or visuotactile condition ($r = 0.087$, $n = 40$, $p = .594$). Similarly, we did not find any significant correlation of the LQ to the agency rating in the active movements condition ($r = -0.118$, $n = 40$, $p = .470$), passive movements condition ($r = 0.086$, $n = 40$, $p = .598$ or visuotactile condition ($r = -0.033$, $n = 40$, $p = .840$). In Exp. 2 we correlated LQ with the proprioceptive drift and found no significant correlation in any of the four conditions: Active synchronous ($r = 0.153$, $n = 20$, $p = .519$), Active asynchronous ($r = 0.397$, $n = 20$, $p = .083$), Visuotactile synchronous ($r = -0.235$, $n = 20$, $p = .319$) and Visuotactile asynchronous ($r = -0.177$, $n = 20$, $p = .456$). Therefore we conclude that handedness did not affect the presented results in terms of subjective strength or proprioceptive drift.

6.1.9.2 The illusion onset

As part of a screening procedure for another study we also tested the onset of the illusion in 128 participants (72 females, mean age = 24,4 years, SD ± 5.2). Participants who experience a clear illusion in the synchronous conditions ($\geq +1$) and deny the illusion in the asynchronous illusion were asked three times to indicate the onset of the illusion (i.e., when they perceive the rubber hand to be their own hand). The average onset during active synchronous movements ($n = 61$) was 23.1 sec (SD 18.5; range: 3.0 - 95.7 sec) and for passive movements ($n = 63$) the average was 22.9 sec (SD 18.4; range: 3.7 - 82 sec). When comparing the average onset time we found no significant difference (Mann-Whitney U Test: $Z = -0.52$, $p = .958$). This suggests similar illusion onset times for active and passive movements conditions.

7 GENERAL DISCUSSION

The presented experiments demonstrate that movements can reliably induce the rubber hand illusion and the moving rubber hand illusion obeys perceptual rules akin to the classical version. Naturally, some findings are in line with previous observations and frameworks, some findings do not agree with previous results, and some findings leave questions open for further investigations.

7.1 THE OWNERSHIP ILLUSION BY MOVEMENTS

Based on our observations we can conclude that movements can induce a strong ownership experience, fully comparable to the classical version of the rubber hand illusion. Although we found that the subjective experience of ownership can be sometimes stronger in the active movements conditions, which would argue for the contribution of agency mechanisms to the sense of ownership, we could not replicate this tendency using the proprioceptive drift measure or the onset measurement. Therefore we conclude that the ownership illusion is equally strong across induction types, and that the moving rubber hand illusion appears to be very similar to the classical illusion.

This is further supported by our observations that the moving rubber hand illusion obeys similar perceptual rules to the rubber hand illusion. Like the classical version of the illusion a temporal rule, a spatial rule and an anatomical plausibility rule can be observed here as well. When the feedback is asynchronous, the distance between the hands is increased, or the model hand is placed in an implausible (rotated) position, the illusion of ownership cannot be induced. The overall similarities are striking, considering the differences between the moving and classical illusion. In the moving rubber hand illusion not only the sense of agency is present, but also the movements generate a very different kind of sensory input. Instead of two rather discrete sensory events (i.e., the vision of the brush touching the rubber hand and the felt touch on the real hand) the moving rubber hand illusion generates a richer set of sensory inputs. Kinaesthetic input like skin stretch, muscle spindles and joint receptors signal the on-going movement (Edin & Abbs, 1991; Edin & Johansson, 1995; Proske & Gandevia, 2012), complemented by efferent signals in the active movements, which could also contribute to kinaesthesia (Christensen et al., 2010; Gandevia, Smith, Crawford, Proske, & Taylor, 2006; Matthews, 1982). Still, the moving rubber hand illusion obeys an analogous set of perceptual rules. This suggests that irrespective of the sensory modality, a similar, if not identical, mechanism generates the experience of ownership by integrating different sensory input from the body. In light of these findings it can be speculated whether the illusion in the moving rubber hand illusion also recruits similar neural structures like the classical illusion (Ehrsson et al., 2004). Given the role of structures like the premotor and posterior parietal cortex for motor control (Culham & Valyear, 2006; Fogassi & Luppino, 2005; Rizzolatti & Luppino, 2001), it seems likely that these structures are involved in the moving rubber hand illusion as well. A possible interaction between ownership and agency mechanisms may be very well mediated by these structures.

7.2 AGENCY IN THE RUBBER HAND ILLUSION

A fundamental difference between the moving and classical rubber hand illusion is the presence of the sense of agency. This requires active movements, where the participant forms motor intentions and receives sensory feedback that matches the motor intentions. This speaks for the involvement of efference copy mechanisms and sensorimotor contingencies in the sense of agency in the moving rubber hand illusion (David et al., 2008; Frith, Blakemore, & Wolpert, 2000b). Both the lack of motor intentions and discrepant (i.e., temporally delayed) sensory feedback affects the sense of agency, but the former is more critical in the generation of agency. In passive movements the sense of agency is more reduced than with asynchronous feedback. In asynchronous movements the agency experience can be relatively high, as compared to passive conditions. This highlights the role of motor intentions in the experience of agency (Haggard, 2005). Unlike the sense of ownership the rotation of the model hand did not change the experience of agency. Participants experienced agency in both these two situations. Therefore we conclude that agency can be detached from ownership of the model hand and experienced in two different contexts: agency over an embodied entity, when participants feel ownership at the same time; and agency over a disembodied entity, so without ownership. The difference between these two situations has been rarely investigated and clarified (S. Gallagher, 2007; 2012; Sperduti, Delaveau, Fossati, & Nadel, 2011; Tsakiris & Haggard, 2005a). To gain clarity about what “internal agency” or “self-agency” refers to and what distinguishes it from “external agency” one could define internal agency as agency in an embodied context, so including the experience of ownership. Whether this definition matches other concepts like "self-agency" or "feeling of agency" needs further investigation. Future research could examine whether these two contexts imply different neuro-cognitive mechanisms. This could help to understand some of the discrepancies found in the previous literature. Importantly, this should be re-examined with an objective measure of the sense of agency, which we did not use in the present of line work.

These investigations could also examine spatiotemporal thresholds like in classical agency paradigms outlined before (see Section 3.2), but including a clear operationalization of ownership and agency. Shimada and colleagues (2009) examined whether detection thresholds differ between active and passive movements, therefore examining the role of agency related mechanisms for the threshold detection. They did not find a significant difference in the absolute threshold, but in the steepness of detection curves (Shimada, Qi, & Hiraki, 2009b). Following this line of thought we plan to examine whether the temporal threshold in a mismatch detection paradigm changes when participants not only feel agency over the visually observed hand movements, but also ownership.

7.3 HOW DO OWNERSHIP AND AGENCY INTERACT

The dissociability of ownership and agency raises interesting questions about the nature of their relationship and their contribution to bodily self-recognition. Our results suggest that ownership and agency can be dissociated: Ownership can be experienced without agency (i.e., in passive movement conditions), but agency can be experienced also without a feeling of ownership (i.e., in the incongruent conditions). At the same time we also found indications for interactions: ownership seems to increase the tendency for agency, but agency does not lead to ownership per se. That ownership might automatically increase the tendency for agency is conceivable: we normally experience our body by movements and our ability to control these movements. Therefore, anything that is perceived to be part of my body should also be movable and controllable. At the same time if we think of a switch, which we can use to control a light bulb, we do not necessarily would feel the light bulb to be part of our body despite the fact we are perfectly able to control it. Thus, agency must not automatically generate ownership.

Our observations do not agree with previous conclusions on the relationship of ownership and agency. Tsakiris and colleagues (2007b) suggested that the "…*Sense of agency normally implies ownership (one knows one is controlling one's own body), but ownership does not imply a sense of agency since the presence of self-generated movements is necessary for the sense of agency, but not for body-ownership.*" (p. 647). Our results do not directly comply with this conclusion, because the sense of agency can be detached from ownership and experienced without a sense of ownership. Ownership might also increase the tendency to experience agency, with the obvious restriction that movements need to occur to generate a full-blown experience of agency.

Later, Tsakiris and colleagues (2010) hypothesized two principal models that could describe the relationship of ownership and agency: an additive model, which suggests that both ownership and agency are related to each other, versus an independence model, in which both ownership and agency are distinct and separated experiences with no direct overlap. The results are mixed in a way that the behavioural data (i.e., subjective experience) would speak for an additive model with agency facilitating ownership (as indicated by higher ownership ratings). The results of the imaging experiment did not reflect this interactive process and would rather speak for an independent model of ownership and agency. One reason for this result could be the specific design of the experiment in which agency was always experienced in the context of ownership, thus never detached from ownership. Therefore, the contribution of each of the two processes might be still not completely separated.

In a certain way our observations concur with both an additive model and independence model of ownership and agency. This could potentially be explained by the two different definitions of agency (Internal versus External), as outlined above.
This conclusion may be important when re-examining the question of how ownership and agency interact. Our results suggest that ownership and agency can be related to each other, but in a directed way: ownership facilitates the (internal) sense of agency, but the (external) sense of agency must not facilitate the sense of ownership per se. A sense of agency alone does not imply ownership, as agency can be experienced without ownership over an internal object (external agency). Further investigations are needed to clarify the interaction between ownership and the two potential types of agency.

So, does ownership increase during movements as compared to the non-moving classical rubber hand illusion? Our results here were mixed, in line with the mixed results in the previous literature. When looking closer at our data, it often seems that ownership is higher during active than in passive movements. At a first glance this suggests that efference mechanisms contribute to the ownership sensation. However at the same time we also observed no differences between active movements and visuotactile stimulation. Other measures like the proprioceptive drift or the onset measurement also do not show this tendency for a stronger illusion in the active conditions. Other studies likewise did not find a difference in the strength of the illusion between the three induction types (Tsakiris et al., 2006), whereas others found indications for a stronger illusion in active movements (Dummer et al., 2009).

If efference copy mechanisms facilitate the integrative process underlying the illusion, why do not we see also that active movements lead to a stronger illusion than the classical illusion? A way to reconcile these somehow contradicting observations is to consider the following speculation: in all three induction types we have a set of differing sensory input, which needs to be evaluated for coherence. In active movements we have kinaesthetic information from a variety of somatosensory input and efference copy mechanisms. In the passive movement we have the same kinaesthetic input, but lacking the efference copy. And finally in the classical illusion we have only two distinct sensory inputs (i.e., touch and vision). However, this must not mean that the condition with the highest number of available input (i.e., the active movements) will lead to the strongest illusion. A higher amount of sensory input means also a higher degree of noise (Faisal, Selen, & Wolpert, 2008), which adds processing demands especially for sensorimotor control (Harris & Wolpert, 1998). In the end the increased number of sensory input inevitably results in much more sensory noise to deal with. This can pose a problem when considering the statistical nature of perceptual processes (Ernst & Banks, 2002; Friston, Kilner, & Harrison, 2006; Knill & Pouget, 2004).

A different, but related hypothesis why the illusion does not differ between induction types can be formulated when we assume that the central process underlying the illusion collects sensory signals until enough “evidence” is accumulated. Once enough sensory “evidence” is accumulated, meaning here correlated multisensory signals related to the hand, the illusion would be generated. In this way the illusion may not be dependent on the specific pairings of multisensory stimuli, but on their mutual correlation and predictability.

Future research could examine which modalities are critical or necessary for the illusion and how the perceptual weighting of this input in relation to sensory noise affects the integrative process underlying the illusion. Differences in the integration of multisensory stimuli could relate to interindividual differences in terms of susceptibility to the illusion. This could potentially explain why some participants might be particular responsive to one type of stimulation and why some participants are not experiencing the illusion at all.

7.4 IMPLICATIONS FOR CLINICAL RESEARCH

7.4.1 Clinical disturbances in body perception

Neurological disturbances of the perception of the own body are multifaceted syndromes, including ownership and agency abnormalities. The involvement of structures like the premotor, posterior parietal cortex (in particular inferior parietal regions) and the insula in pathologies affecting the perception of the body like anosognosia or asomatognosia has been confirmed by a number of studies (Baier & Karnath, 2008; Berti et al., 2005; Karnath & Baier, 2010; Orfei et al., 2007; Zeller, Gross, Bartsch, Johansen-Berg, & Classen, 2011). At the same time we know that these structures are involved in the generation of ownership and agency (Brozzoli et al., 2012; Ehrsson et al., 2004; 2005; Farrer et al., 2003; Farrer, Frey, Van Horn, Tunik, Turk, et al., 2008b; Tsakiris et al., 2007a). The question arises how and where these aspects interact at the neural level when we perceive our own body moving. The present results might help to further clarify the exact relationship between ownership and (internal and external) agency also at a neural level by examining these functions with imaging techniques like fMRI or EEG. These insights could further elucidate these pathologies and help us to understand why patients exhibit certain pathologies. This could also elucidate why, for example, anosognosia and asomatognosia co-occur after lesions in the insula (Baier & Karnath, 2008), but anosognosia appears after lesions in the premotor cortex (Berti et al., 2005). A deeper investigation of ownership and agency at a behavioral and neural level with healthy participants might help us to better understand these observations in these patients.

The present rubber hand illusion paradigm could be a useful new tool to investigate the breakdown of ownership and agency in psychotic disorders, in particular schizophrenia. A leading hypothesis for a decade has been that some of the symptoms of schizophrenia might be explained by the breakdown in comparator mechanisms related to the sense of agency (Franck et al., 2001; Frith, Blakemore, & Wolpert, 2000b; Haggard, Martin, Taylor-Clarke, Jeannerod, & Franck, 2003; Shergill et al., 2005; Synofzik, Thier, Leube, Schlotterbeck, & Lindner, 2010; Voss et al., 2010), resulting in delusions of control and passivity symptoms (Frith, 2005a; 2005b; Jeannerod, 2009). Recently schizophrenia researchers have also started to investigate the domain of body-ownership and possible impaired mechanisms of body representation by using the rubber hand illusion paradigm (Germine et al., 2012; Peled et al., 2000; Thakkar et al., 2011). Having said that the question arises how these disturbances of agency and ownership might interact to eventually result in the problems of self-recognition seen in psychotic disorders. Given that psychotic patient do not only have a distorted experience of agency, but also ownership (Waters & Badcock, 2010).

From this perspective the present moving rubber hand illusion set-up could be a useful new approach for cognitive schizophrenia research to combine measurements of ownership and agency in a single paradigm and further explore how psychotic traits affect the experience of the own body or vice versa. As illustrated by Study IV not only psychotic patients, but also delusion-prone participants might already exhibit certain abnormal tendencies in their experience of their body. An interesting question can be formulated by asking whether self-recognition disturbances seen in schizophrenia are a result of changes in ownership and / or agency, and how both these processes interact when prodromal individuals converge to a clinically manifest psychosis. Future research could explore the factors behind psychotic disorders by using bodily illusions like the moving rubber hand, which tap more specifically into the mechanisms of self-recognition by combining ownership and agency.

7.4.2 Research on neuroprosthetics

Recent years have seen increasing interest in how one could design advanced prosthetic limbs that would feel and act more like real limbs. These limbs could be controlled by brain-computer interfaces (Hochberg et al., 2006; Nicolelis, 2003; Schwartz, 2004; Velliste, Perel, Spalding, Whitford, & Schwartz, 2008), myo-electrically controlled

(Marasco, Kim, Colgate, Peshkin, & Kuiken, 2011), or be traditional cosmetic prostheses (Ehrsson et al., 2008). Regardless of the technical design and degree of invasiveness it seems reasonable to assume that the user would benefit from experiencing both ownership and agency of the artificial limb. The basic cognitive and neuroscientific constraints of ownership and agency, as explored here, could thus be taken into account when developing the next generation of advanced prosthetic devices. That these insights from non-amputated participants can be transferred to the amputees is seen by the fact that the rubber hand illusion can be induced in amputated participants. The tactile stimulation is applied here at the place of the stump where the participants report a referred sensation to one of the digits, and to the corresponding digit of the rubber hand. Similar to non-amputated participants also amputees report similar sensations of ownership after synchronous, but not asynchronous stimulation (Ehrsson et al., 2008; Rosén et al., 2009; Schmalzl et al., 2011). A case study using fMRI suggests that also in these participants a premotor-posterior parietal network is activated during the illusion (Schmalzl, Kalckert, Ragnö, & Ehrsson, 2013).

A critical step here is the development of sensory feedback from the prosthesis. Sensory feedback is necessary to create a sense of ownership towards the artificial limb, but equally important for motor control (Johansson & Flanagan, 2009). Also here recent technological advances in providing such tactile feedback offer promising new developments (see i.e., Raspopovic et al., 2014), which can lead to a new form of prosthetic devices in the not so distant future. Once these technological advances will become part of general therapeutic strategies in the care of amputated patients, the experience of ownership and agency towards the prosthesis would help the user´s overall well being. These experiences might restore a more complete and coherent perception of the own body and increase acceptance of the prosthesis (P. Gallagher & MacLachlan, 1999).

Similarly the present results could be useful to optimize the sense of ownership and agency in virtual-reality to give people simulated limbs and bodies (Slater et al., 2008; Slater et al., 2009; Perez-Marcos et al., 2009; Sanchez-Vives et al., 2009). These techniques create new avenues in the therapeutic and rehabilitative strategies for patients with physical or psychological disorders related to their experience of the body or self (Sanchez-Vives & Slater, 2005).

7.5 FUTURE DIRECTIONS

The present work provides a first attempt to systematically study the problem of bodily self-recognition by combining ownership and agency in a single paradigm. The combination of both these aspects offers promising new insights into the perceptual mechanisms underlying bodily self-recognition. Naturally there is room for improvement and refinement of the presented paradigm and several unanswered questions to be addressed in the future.

One important question relates to how efference copy mechanisms contribute to the ownership sensation. To answer this question we need to explore further potential differences between active and passive movements, which is the best and most elegant way to disentangle the contribution of afferent and efferent information. An important aspect here would be to find a way to perfectly match active and passive movements in terms of movement kinematics, considering the manual procedure used in our studies. This could be realized by new robotic devices, which are able to copy movement parameters from the participant´s hand movements. One other way to address this question is also to investigate how processes related to agency, like basic sensorimotor control mechanisms, transfer to the rubber hand during the illusion.

Based on our observations we proposed that agency could be differentiated in two different types: internal versus external agency. This question is now open for future experiments to characterize both these types of agency, and find ways to differentiate between agency towards the body and agency towards objects in the external world. This might also help to elucidate some of the inconsistencies in the previous literature, which often appears unclear in this matter. To this end we are currently preparing an experiment, which allows temporal and spatial manipulation of visual feedback of hand movements. Given that ownership and agency can be isolated we can create experimental situations, in which the participant experiences agency and ownership versus situations, when the participant experiences only agency without ownership. Thus, it can be directly tested whether temporal thresholds differ in these two contexts.

Related to this is also the need for a robust objective measure of agency that could be combined with the presented rubber hand illusion paradigm. It would be interesting to see whether this objective measure would reproduce the observations we have made so far by using subjective measures of agency.

Finally, it would be interesting to describe the neural correlates of the moving rubber hand illusion. Previous research indicated that a fronto-parietal network is involved in the illusory experience of ownership over the rubber hand (Brozzoli et al., 2012; Ehrsson et al., 2004; Gentile et al., 2013). This network is also particularly important for motor control. This might pose a challenge to disentangle these motor control processes and the neural correlates of ownership, while moving a rubber hand that feels like your own. The large similarities between moving and classical illusion suggests that similar perceptual, and with this possibly similar neural processes underlie the illusion.

In conclusion, there are new questions about the nature of ownership and agency, which need to be addressed and for which the present work represents a modest attempt to achieve some answers. Still there is a good reason to believe that our results contribute to our knowledge of the mechanisms underlying bodily self-recognition.

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